BOTANICAL GAZETTE

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THE BOTANICAL GAZETTE

EDITOR
JOHN MERLE COULTER

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JULY–DECEMBER, 1912

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ERRATA

P. 1, to title add index[1], and append footnote Contribution from the Botanical Laboratory of the Johns Hopkins University, No. 24.

P. 51, line 3 from bottom, for than read then.

P. 57, line 14 from top, for carpel read carpels.

P. 79, footnote 2, for VOLGER read VOGLER.

P. 88, footnote 34, for COMBES, RAOUT read COMBES, RAOUL.

P. 127, change lines 14–20 to read as follows: be 1 white-flowered to 1 purple-flowered, or in this particular family 13 white-flowered to 13 purple-flowered, to which expectation the observed result is not in sufficiently close agreement even considering the small number of individuals. If the *rubrum* parent were heterozygous in respect to both the primary factors for color, *C* and *R*, it being assumed that the *album* parent lacked both these factors, a 3:1 ratio would result.

P. 127, line 28, omit also.

P. 148, line 19, for CASTILLEJA VISCIA read CASTILLEJA VISCIDA.

P. 164, line 19, omit on before *Griffithsia* and *Delesseria*.

P. 164, line 21, insert regularly before borne.

P. 165, legend of fig. 1, for a *Polysiphonia* (?) read the plant referred to in this note.

P. 191, last line, for Eracheinungen read Erscheinungen.

P. 208, line 8, for practically read partially.

P. 235, line 8 from bottom, omit hyphen between subtus and fusco.

P. 252, line 11, for 37.095 read 37.95.

P. 269, line 13, for into read in to.

P. 274, line 11, for slight read slightly succulent.

P. 277, line 1 of *Celtis* table, for (87–72) read (27–72).

P. 281, line 1 of *Ostrya* table, for (66–95) read (66–93).

P. 297, line 11 from bottom, after reported insert (**3**).

P. 393, line 2, for began read begins.

P. 405 for **Calochortus umbellatus** read **Calochortus euumbellatus;** line 10 from bottom, for *C. umbellatus* read *C. euumbellatus.*

P. 419, line 5, for in the Tropic read on the Tropic.

P. 428, footnote 2, for 1912 read 1911.

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July 1912

Editor: JOHN M. COULTER

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Briefer Articles
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THE

BOTANICAL GAZETTE

JULY 1912

THE DEVELOPMENT OF THE VASCULAR STRUCTURE OF DIANTHERA AMERICANA

W. RALPH JONES

(WITH PLATES I–IV)

In 1907, THEO. HOLM (**5**), in describing the anatomical structure of *Dianthera americana*, called attention to the "polystelic" condition of the stem. This paper seems to be the only one ever published on this intensely interesting plant. So at the suggestion of Professor DUNCAN S. JOHNSON, I have made a study of the ontogenetic development of the stelar structure in order to find out how the "polystelic" condition of the mature plant is derived.

The material studied consisted of seedlings grown in the laboratory and greenhouse from seeds collected near the Chain Bridge (over the Potomac River about four and one-half miles above Washington, D.C.), of seedlings collected at the Chain Bridge, and of mature plants from Chain Bridge and from near Betterton, Md.

Most of the material studied was imbedded in paraffin, and sectioned 5–10 μ thick. Various stains were used, but the best results were obtained with methyl green and acid fuchsin.

Dianthera americana is a perennial herb, with an erect stem 3–9 dm. high, grooved and angled, usually simple, and having opposite, simple, linear-lanceolate leaves 75–150 mm. long and 6–15 mm. wide. At the Chain Bridge, the plant grows in the tide pools on the rocky flats on the north side of the river, and also along the banks of the Chesapeake and Ohio Canal, which at this point runs parallel to the river just back of the flats. The plant produces flowers from May on through the summer, ripening its fruits from

about the middle of July to the end of summer. The fruit, a loculicidal two-celled capsule, dehisces violently, often throwing the four seeds a distance of several decimeters. The seeds germinate very soon after being shed, the seedlings reaching a height of about 2 dm. by the end of the growing season. Branches formed in the axils of the basal leaves, and at first growing upward, soon curve, and grow downward to just below the surface of the water, then take a nearly horizontal direction. These stolons, becoming 0.5–1 dm. long, send out adventitious roots at the nodes that pass downward into the mud.

At the end of the growing season, the vertical shoot dies down to just below the usual level of the water, usually to the top of the first node below the surface. The rest of the stem remains green and apparently in good condition for some time, but gradually rotting. The stolons, with their scalelike leaves, where exposed to the light, remain green throughout the winter, as do also the upper parts of the adventitious roots. In the spring, the terminal bud of the stolon again starts its activity, turning upward, and sending up a vertical shoot into the air. This shoot develops elongated leaves, and rarely branches from near the base. The basal buds, however, usually produce the rhizomes by means of which the plant perennates. Buds formed in the axils of the upper leaves develop into the capitate-spicate inflorescences of violet or nearly white flowers.

At Betterton, Md., the plant grows under different conditions. Instead of growing in the water, it grows in the sand just above the level of high tide; the rhizomes grow about on the level of the top of the moist sand, the lower one to three internodes of the aerial shoot being buried in dry sand. The basal branches grow upward a few centimeters, turn down, and then become horizontal, growing along the top of the moist sand at a depth of 5–10 cm. below the surface. The basal part of the erect shoots and also the rhizomes, therefore, are without chlorophyll. Although many discharged capsules were seen, I could find no trace of seedlings, so I cannot say that the life-history here is the same as at Chain Bridge, but from the time of flowering and of the ripening of the seeds, and from the general habit of the plants, I see no reason for believing that there are any marked differences in the general life-history.

As HOLM (5) has pointed out, both the vertical aerial stem and the horizontal submerged rhizome show, in a cross-section of an internode, six peripheral and one central bundle, each of leptome, hadrome, and pith, and each completely surrounded by a thin-walled endodermis, each having, therefore, the appearance of a complete stele (fig. 8). For this reason, HOLM says that the plant is polystelic; from its development, however, it will be seen that it is really astelic.

At each node there is a fusion of the six peripheral meristeles to form a complete ring of vascular tissue, which breaks up in a very regular way to form the six peripheral meristeles of the internode above (fig. 1). Each of the bundles of the lower internode divides at the node to form a Y; then each branch fuses with a branch of the adjacent Y, thus giving rise to the six peripheral bundles of the next internode. The single leaf traces join the vascular system of the stem at the crotches of two opposite Y's. The two bundles which supply the traces are usually, though not always, larger than the other four. There is also a connection made, at each node, between the central bundle and the peripheral ring of vascular tissue by means of a transverse arm, coming out from the central bundle at right angles to it and fusing with the vascular ring just below the insertion of the leaf traces (figs. 3–8 show a series of transverse sections through the node). The structure of the node next above or next below the one described is exactly the same, except that its plane of symmetry is at right angles to that of the adjacent one, as is shown in fig. 1. A diagram of the path of the bundles in a mature plant is shown in fig. 2.

The seeds

The seeds (figs. 11 and 12) are much flattened, and are nearly circular in outline. They are about 2–3 mm. in diameter, and about 0.75–1 mm. in thickness. On the lower side the edge of the seed is slightly hollowed out to form a pocket in which lie the hilum and the micropyle. The testa is brown in color, and has a much roughened surface, owing to the distortion of the underlying cells, of which there are two to four layers (fig. 10). The walls of the epidermal cells are thickened in bands which fuse at some places, and at others taper to a point and disappear. The inner

cells are thin-walled, and are much distorted in shape. The endosperm is represented by a thin pellicle, usually two cells in thickness, except at the lower edge of the seed, where it thickens to form a mass of appreciable thickness, which forms a cap over the free end of the hypocotyl. The well developed embryo nearly fills the seed. The two large cotyledons are flat, nearly circular in outline, accumbent, the curved hypocotyl lying closely against the edges of the cotyledons, and being free only at the end. The seed, therefore, corresponds very closely to that of *Dianthera nodosa* Benth. & Hook. as described by SCHAFFNIT (**8,** p. 65).

The epidermis of the hypocotyl is composed of small cells which are elongated vertically. The cortex consists of about ten layers of cells, radially arranged, and of larger diameter than those of the epidermis. They are flattened vertically, and appear nearly square in cross-section. The innermost layer appears in no way different from the rest of the cortex. One striking feature of this layer, however, is the division of its cells, on each side of the central cylinder between the protoxylem poles, to form two layers (fig. 14). Schizogenous air cavities, of small diameter, but of considerable length, have already formed between the angles of the adjoining cells.

The central cylinder is sharply marked off from the surrounding cortex, owing to its greatly elongated cells of very small diameter (fig. 14). Just below the insertion of the cotyledons, the central cylinder divides to form the two procambial cotyledonary traces (fig. 13).

Germination

The earliest stages of germination have not been observed in the field. Seeds brought into the laboratory and soaked in water swelled about 0.5 mm. in diameter and about 0.25 mm. in thickness. These soaked seeds were then placed in a moist chamber, either on wet filter paper or on wet sand. The testa soon split, the hypocotyl pushing through. Further growth now forces upward the upper end of the hypocotyl and the cotyledons, often carrying the testa still clinging to one or both of the cotyledons. The latter soon become green, continue their growth, and function photosynthetically for some time. The plumule is rather tardy in starting its growth.

For ease of description, we will divide the growth of the seedling into stages corresponding to the number of pairs of leaves present.

STAGE I

The first seedling stage (fig. 15) shows the elongating hypocotyl well out of the testa, pushing upward the cotyledons which are frequently still inclosed within the testa. All the endosperm found in the seed has been used up. The primordia of the first pair of leaves are beginning to develop, but no sign of differentiation of the foliar traces has yet appeared. From each cotyledon one double bundle enters the hypocotyl (fig. 16). These bundles approach each other, and very soon come together to form the central cylinder.

In the middle of the hypocotyl, a cross-section shows an epidermis of cells slightly elongated radially, the inner and side walls thin, the outer walls slightly cutinized; the cortex, about 10–12 cells in thickness, the outer two or three layers of irregularly arranged cells, which are beginning to show a slight thickening and later forming a typical collenchyma. The remaining inner layers of the cortex are made up of rounded thin-walled cells, very regularly arranged in radial rows, their walls being in contact except at the angles, where there are formed small schizogenous air cavities, which latter extend vertically for a considerable distance. The innermost layer of the cortex is not modified in any way, being like the other cells of the inner part of the cortex in size, shape, and content of cells.

The central cylinder, or stele, is very sharply marked off from the surrounding cortex, being made up of much smaller cells except at the very center. The pericycle is of one layer except opposite the xylem poles, where it is of two layers. The xylem is arranged in two opposite groups, the protoxylem being exarch. The four phloem groups are placed one on each side of the xylem poles. The rest of the central cylinder is of thin-walled parenchyma, small near the periphery, but becoming much larger at the center. There are no air spaces in the central cylinder.

Transition.—In the petiole of each of the cotyledons is a double bundle, the protoxylem of which occupies an endarch position. As the two bundles of the cotyledons enter the hypocotyl, there is

a rotation of the xylem, the protoxylem becoming exarch. On reaching the transition region, near the base of the hypocotyl, the phloem of each bundle divides, and passes to the right and left of the xylem. Each half moves to the side of the stele, finally fusing with a half of the phloem from the other bundle. This forms a typical diarch root, the transition being that of Type III of VAN TIEGHEM. Fig. 17 shows a diagram of the path of the vascular tissue at this stage.

STAGE II

In the second stage, the first pair of leaves have enlarged sufficiently to be seen easily by the naked eye (fig. 19). The primordia of the second pair of leaves are not differentiated until near the end of this stage. The bases of the cotyledons have fused to form a short tube. The leaves of the first pair are opposite and are decussate to the cotyledons. As they develop, there begins the differentiation of a single vascular bundle for each, the differentiation beginning at the node, passing outward into the leaf, and downward into the stem, passing through the very short epicotyl into the hypocotyl, and becoming inserted between the cotyledonary bundles, the protoxylems finally disappearing near the base of the hypocotyl.

There have also started to develop two buds, one axillary to each cotyledon, but at this stage neither shows any differentiation of vascular tissue. A diagram of the course of the vascular tissue at this stage is shown in fig. 18.

The cortex and epidermis are very nearly as in the preceding stage, the angles of the outer cortical cells being more thickened, however, and the outer wall of the epidermal cells being heavier than before. Glandular hairs of the type found on the mature plant (figs. 26 and 27) are numerous on the hypocotyl and cotyledons.

At the close of this period of development, a bundle develops on each side of the stem between the two traces of the first pair of leaves. These bundles, at the lower end, are forked just over the cotyledonary traces, the forks being inserted on either side of the traces, between them and the bundles from the first leaves. At the upper end, the bundles fork, the branches passing off nearly

at right angles to the main bundle, and being inserted on the sides of the leaf traces of the first pair of leaves. There is thus formed a complete ring of vascular tissue in the first epicotylar node. Rarely the forks at the base of the bundles are of very unequal size, or one of the bundles may even fail to divide, in this case merely bending aside, and becoming inserted on one side or the other of one of the cotyledonary traces. The direction of differentiation of these side bundles seems to be acropetal, but this could not be made out definitely. The cross-arms connecting the bundles with the traces of the first pair of leaves, however, are undoubtedly younger than the main part of the bundles. Fig. 20 shows the course of the bundles at this stage.

STAGE III

With the development of the second pair of opposite leaves at right angles to the first pair, and directly over the cotyledons, we have the third stage (fig. 22). At the insertion of each of these leaves, there starts to differentiate a single bundle, passing outward into the leaf, and downward through the stem, becoming inserted in the crotch of the fork of the bundle just developed at the close of the preceding stage (fig. 21).

If we now examine this latter bundle (fig. 23), we find that it possesses three protoxylem elements, one being derived from the newly developed trace of one of the second pair of leaves, the other two connecting, one through each of the horizontal connecting branches, with the outgoing leaf traces of the first pair of leaves. At the lower end of the bundles (figs. 24 and 25), one of the protoxylems passes out along one of the forks; the other two, which have been closely applied to each other throughout the whole length of the bundle, pass out the other. These bundles at first have the appearance of being double, the two parts being separated by a narrow parenchymatous (medullary ?) ray, but being, later at least, entirely surrounded by a complete endodermis.

A cross-section (fig. 28) through the middle of the second epicotylar internode shows an epidermis, or rather protoderm, of thin-walled cells, sharply marked off from the internal cells. Within this protoderm is a meristematic tissue of cells practically all alike, showing no differentiation into cortex and central cylinder,

and with no air spaces. In this ground tissue are imbedded the two procambial strands of the traces of the second pair of leaves.

In the middle of the node below, there is to be seen a ring of vascular tissue inclosing an area of rounded parenchymatous cells similar in appearance to the cortical cells surrounding the vascular tissue. The inner layer of the cortex differs from the remaining cortical cells only in being more tightly placed together, thus forming a sheath. There is as yet no thickening of the walls of the cells forming this sheath.

Immediately below this node, the sheath sinks in between the four bundles, breaks, the ends turn in and form a complete sheath around each of the bundles, inclosing also a small amount of the undifferentiated parenchyma (pith?) on the inner face of each bundle. This condition persists throughout the internode. At the forking of the two opposite side bundles (figs. 24 and 25), the sheath sinks in between the forks, and so forms a complete sheath around each branch. On entering the cotyledonary node, these sheaths break on the inner face of the bundles, open out, the ends of each fuse with those of the adjacent bundles, forming thus a complete, but at first irregular, sheath around the entire central cylinder of the hypocotyl, which sheath continues downward into the root. At places, the bundle sheaths in the basal epicotylar internode show the characteristic Casparian dots on the side walls; this is also true of the sheath around the central cylinder of the hypocotyl and root. At this stage, however, the sheath is extremely irregular, being often of two layers for a short distance, and in most places showing no special endodermal characteristics.

A cambium has appeared in the bundles from the first pair of leaves, but very little secondary tissue has as yet been formed. In the hypocotyl there is a much interrupted cambium which has formed a little secondary tissue. At a later stage, the cambium forms a complete ring, and so develops a complete ring of secondary vascular tissue. In the root there is now to be found an interrupted cambium, which later becomes complete except at the protoxylem poles. The older primary root, therefore, will have two crescent-shaped masses of secondary tissue, the horns of which come together opposite the protoxylem poles.

The buds, found at the preceding stage in the axils of the cotyledons, have developed somewhat, each having now two very small leaves, each of which furnishes a single trace which passes downward into the hypocotyl. These become inserted, one on each side of the cotyledonary trace, between it and an arm of the forked bundle entering from above.

The bases of the first pair of leaves were at first distinct, but they have by this time grown together to form a short tube. This is the case with all the later formed leaves. A bud is starting to develop in the axil of each of the first pair of leaves, but at this stage has developed no vascular tissue.

From now on, the order of differentiation of new bundles is the same as that just described. At the close of each stage, there develops a pair of opposite bundles, each double in appearance, having two groups of protoxylem and protophloem elements separated by a parenchymatous ray. These bundles fork below, the forks being inserted between the traces of the underlying pair of leaves and those of the latest formed pair. Above, the bundles fork, connecting with the outgoing, latest formed leaf traces. In the next stage, these bundles become surrounded by a sheath which finally develops into a well marked endodermis. At the beginning of each stage, there is differentiated a trace from each of the newly formed leaves, which trace passes downward to the node below, being there inserted in the crotch of the underlying forked bundle which has just been developed at the close of the preceding stage.

The central bundle

The earliest sign of any medullary vascular tissue is to be found in a single example of a fourth-stage seedling, where, in the first epicotylar node, there are traces of medullary phloem. The course and attachment of these medullary phloem strands (fig. 30) are best described by starting with the conditions found just below the node, and following these upward through the node.

As the four bundles found in the basal epicotylar internode spread out on entering the node to form a complete ring, three protophloem elements from the peripheral vascular tissue pass inward toward the center. One of these protophloems arises from

the side of one of the leaf traces of the first pair of leaves. This single protophloem element passes inward toward the center of the ring. It never reaches it, however, but turns upward, and disappears in the middle of the node. The other two protophloem elements arise, one from the side of the other leaf trace, and the second from the adjacent face of one of the side bundles. These pass toward the center, become applied to each other, and pass vertically upward for a short distance; one disappears, the other soon turns, and passes back to that side of the stem on which it arose, becoming inserted, at the top of the node, on one of the "forks" on the side nearest one of the descending traces of the second pair of leaves.

In a very similar case found in a fifth-stage seedling, a single protophloem passes off toward the center from each side of each leaf trace. These four protophloem elements pass toward the center and turn upward, then turning back to the ring, each fuses with one of the descending forks, just as these enter the ring at the top of the node. In these two cases, the medullary vascular tissue is all entirely intranodal, there being no trace anywhere except just within the one node.

In the fifth stage, however, there is usually developed the central bundle of both xylem and phloem, passing from one node to the next. There is considerable irregularity in its formation, some of the fifth-stage seedlings being entirely without any medullary vascular elements. Taking a seedling where the central bundle has developed, we find, at the third node back from the apex, an elliptical vascular ring surrounded by a well marked sheath which usually, at this stage, does not possess any special endodermal characters. There is no sign of any internal endodermis in this node.

In passing downward out of this node, just as the vascular ring breaks up into four bundles, from one edge of one of the side bundles, a small group of phloem and xylem elements passes inward, free from the outer ring, to the center of the pith, meeting there another group of vascular tissue, which has broken off from the other end of the same side bundle. At a more mature stage, the medullary bundle may be derived from four sources, one at each end of each of the side bundles.

At this stage, the oblique cross-arms are imbedded in the parenchymatous tissue, there being no trace of any sheath. After turning so as to pass vertically downward, the fused bundles become surrounded by a more or less well marked sheath, which soon shows the characteristic Casparian dots on the side walls of the cells. Just above the node below, most of the vascular elements have died out, there being left only three or four phloem elements. These lose their surrounding sheath, and pass across to the peripheral vascular bundles at a level where the endodermis surrounding the forks has just broken. The medullary vascular tissue becomes applied to the outer side of one of the forks, on the opposite side of the stem, however, from which it branched off at the node above. Soon after this the nodal ring becomes closed. If we examine closely the upper node, we find that the vascular elements which turn in to form the central bundle may be traced through the node into the forks of the side bundles of the overlying internode.

At the next stage, the central bundle is differentiated in the next internode above in the manner just described, the lower end of this new bundle becoming inserted at the top of the older central bundle between the incoming cross-arms. A cambium makes its appearance in the central bundle and cross-arms about two stages after the differentiation of these bundles. This cambium frequently forms a more or less complete ring. Usually, however, in the seedling stages, the primary xylem and phloem crowd over to one side of the bundle, the cambium coming in as an arc, forming a collateral bundle of exactly the same structure as the peripheral bundle, in spite of its entirely different origin.

The internal endodermis

In the first five stages, the endodermis which surrounds the bundles throughout the internodes disappears from the inner faces of the bundles on reaching the nodes, leaving only an endodermal sheath surrounding the vascular ring in the node. From the sixth stage on, however, it is usual for the endodermis to be continuous through the node, both externally and internally.

Taking an older node as a type, we find (fig. 3), just above the node, that every bundle is surrounded by a regular endodermal sheath. The leaf trace sheath is usually well differentiated only

on the abaxial side. The sheaths of the two bundles between which the leaf trace enters soon open, the ends becoming connected so as to form a complete sheath around the two bundles and the leaf trace (fig. 4). The inner face of the sheath now bulges toward the central bundle, finally coming in contact with it, and breaking at the point of contact, thus forming a continuous sheath inclosing a dumb-bell-shaped area, each head consisting of the leaf traces and the two side bundles of the stem, the central bundle in the middle of the connection. The endodermis on each side of each "head" now bulges toward the remaining pair of stem bundles, coming in contact with the endodermal sheaths of the latter, and breaking at the point of contact.

There are thus formed three complete rings of endodermis (fig. 5), one externally surrounding the vascular ring, the other two internal, one on each side of the transverse connecting arms. These connecting arms very soon break, the endodermis sinking in so as to form one sheath around the central bundle, and another lying just internal to the vascular ring (fig. 6). This vascular ring now breaks into four parts, the endodermis sinking in until the external and the internal sheaths meet, then breaking apart, thus forming the four bundles of the lower internode, each surrounded by a complete endodermal sheath (fig. 9).

Late stage of seedling

As has been said, the seedling, by the end of the growing season, attains a height of about 2 dm. Such a plant (fig. 31), possessing about 20 nodes, looks very much like a plant of the "mature" type, but is smaller than the mature plant, and of course differs in not having arisen from a rhizome. At the base, several of the axillary buds have developed to form short, nearly horizontal branches, the rhizomes. At the very base there is a cluster of four strongly developed adventitious roots, nearly surrounding the primary root, which is still less developed than the adventitious roots.

A histological examination shows that the vascular system has developed in the manner already described. The uppermost pair of leaves furnish a single trace each; these pass downward to the

second node, where there has been formed a vascular ring. On passing through this node, we now find a new condition. Instead of the vascular ring breaking into four bundles, two of which fork lower down in the internode, it breaks into four bundles, two of which almost immediately divide, the four forks behaving in the same way, however, as the forks produced at the lower end of the internode of earlier stages (see diagram of path of bundles, fig. 29). This condition is very nearly that which exists in the apex of a mature plant (compare diagram, fig. 2), where the nodal ring breaks up immediately into six bundles, four of which, corresponding to the two forked side bundles, are usually smaller than the other two.

An examination of the lower internodes of this stage (fig. 29), or of the corresponding internodes of the intermediate stages, shows that there is a tendency from the very first for the side bundles to fork at a slightly higher level in each succeeding internode. In the third stage, where these side bundles first come in, there is but a very small amount of parenchymatous tissue inclosed above the leaf traces by these forks, forming small leaf gaps. At each succeeding stage, these gaps tend to be longer when formed. I say tend, for there is considerable irregularity. One of the side bundles may fork about the middle of the internode, while the opposite side bundle of the same internode may not fork until very near the bottom of the internode, or, as before mentioned, may not even fork at all. In any individual seedling there is a gradual transition from the immature seedling condition found in the earliest stages, and hence lowermost internodes, to the nearly mature conditions found in the uppermost internodes of the seedling at the end of the growing season.

The old seedling shows, therefore, a permanent record of its ontogenetic development, slightly obscured, it is true, by secondary thickening. It is comparable in this respect to a fern "seedling," the earliest formed internodes showing the simple (primitive?) type of structure, the later formed ones showing a gradual transition to the mature type. It must be remembered, however, that in the fern, when the mature structure is once formed, the main axis continues its growth, each succeeding internode having the mature

structure. In *Dianthera americana*, on the other hand, the main axis seems never to produce a perfect mature type, but only approaches it. The mature type is here first produced in a branch, the rhizome. When once attained, however, it is persistent, as in the case of the fern.

Owing to the secondary development of vascular tissue, the general appearance of the bundles, or meristeles, has changed considerably. Instead of being strictly collateral, as they were in the earlier stages, there is a tendency for them to become concentric, the xylem and phloem being formed on the sides, and later, by the extension of the cambium, they are also formed on the inner face of the meristeles. The cambium may even form a complete ring, though this is not common in the seedling stages.

The presence of this internal, and of course, inversely oriented mestome, causes the node of an older seedling to have a rather different appearance from that of the young seedling. On entering the node (figs. 3–9), part of the vascular tissue on the sides of the meristeles, sometimes of the phloem only, sometimes of both xylem and phloem, passes around to the inner face, becoming inverted during the passage. Part of the internal mestome of two of the bundles turns into the transverse arm, and so connects with the central bundle. Below the transverse arm there are three concentric rings of endodermis, one external to the complete ring of normally oriented xylem and phloem, the second just within the inversely oriented mestome. The third and innermost endodermis surrounds the central cylinder. The normally oriented mestome is separated from the inverted vascular tissue by a layer, several cells in thickness, of closely packed parenchymatous cells. This layer is continuous with the parenchyma of the individual meristeles, above and below the node. The middle endodermis is separated from the innermost sheath by a layer of cells continuous with the ground tissue of the internode, but much more closely packed together. There is, however, still a considerable amount of air space.

The epidermis and ground tissue of the late seedling are exactly like those of the mature plant. As HOLM has already accurately described and figured these tissues, nothing more need be said of

them. The leaves of the seedlings correspond very closely to those of the mature plant. The latter have been fully described by HOLM. One correction must be made, however. HOLM says (5, p. 326) "collenchyma and stereome seem to be entirely absent from the lateral portion of the blade," apparently overlooking the marginal strand of collenchyma occuring in both seedling and adult leaves (fig. 32).

The axillary buds

It has already been mentioned that buds are usually formed in the axils of the leaves. In most cases, except at the base of the plant, these buds, after having developed one or two pairs of very small leaves, remain dormant. Several of the basal buds may develop, giving rise to the horizontal rhizomes, by means of which the plant perennates. The bud arises as a small mound of tissue in the axil of the leaf. On this mound there soon appear the primordia of a pair of opposite leaves, whose plane of symmetry is at right angles to that of the subtending leaf. A single leaf trace from each leaf is differentiated, and passing downward becomes inserted between the trace of the subtending leaf and an arm of the forked bundle of the stem.

As in the main stem, the next step in development is the differentiation of a pair of forked bundles, the forks of the outer bundle being inserted between the first pair of leaf traces and the trace of the subtending leaf. The arms of the other forked bundle become inserted behind the first pair of leaf traces, between them and the forks of the stem bundle. As in the stem, a pair of traces from the second pair of leaves now differentiate, and become inserted in the crotch at the top of the forked bundles. By this time it is seen that a very irregular sheath is forming around each of the bundles of the lower part of the bud (fig. 33). On entering the node below, these sheaths open on the inside, the ends connecting so as to form a complete sheath surrounding the bundles of the bud and the trace of the subtending leaf (fig. 34). Lower down, this sheath opens on the inside, the ends connecting with those of the opening sheaths of the "forks" of the stem. This forms a complete sheath around all of the bundles, as is shown in fig. 35. The endodermis now behaves in the way already described in a node which had no bud.

The later development of the axillary bud is exactly the same as that of the main stem, with this exception: while in the stem the transition from seedling structure to the mature type is very gradual, the transition in the branch is much more rapid, being completed in about 6–8 internodes. After having once been attained, the mature type recurs constantly in each succeeding internode.

Roots

In the old seedling there are to be found four types of roots, each having its characteristic structure. These are the primary, secondary, and adventitious roots, and the branches of the latter.

The primary root is diarch, maintaining this type of symmetry even when mature. Its growing point is of the "*Helianthus*" type, having distinct plerome and periblem initial groups, while the calyptrogen and dermatogen have a common group of initials. As the root matures, a cambium develops in a ring, broken opposite the two protoxylem poles, forming two crescents of secondary vascular tissue. The stele is surrounded by a sharply defined thin-walled endodermis with Casparian dots. The cortex and epidermis correspond to those of the adventitious roots of the mature plant, sufficiently described by HOLM. He, however, wrongly calls these roots "secondary" (**5**, p. 319).

The true secondary roots, that is the branches from the primary root, possess the same type of growing point as the primary root. The symmetry varies with the age, the younger parts of these roots being usually diarch, and becoming later tetrarch or pentarch. The general structure of these mature secondary roots is that of the adventitious roots. The adventitious roots, formed at the base of the seedling, and the branches of these adventitious roots, are exactly like those described by HOLM for the mature plant. These also possess the "*Helianthus*" type of growing point.

Abnormalities in the internal structure

One very striking feature about the seedlings of *Dianthera americana* is their extreme variability. Two seedlings of the same stage, that is with the same number of leaves developed, may show very great differences in the degree of differentiation of vascular tissue, cambium, endodermis, etc. For instance, a seedling of the

fifth stage may have a better developed endodermis in its basal internode than can be found in an ordinary seedling of the eighth or ninth stage.

One of the most striking abnormalities, however, is the failure of an entire bundle to differentiate. This is frequently the case with the central bundle. This may develop in one internode, fail to do so in the next, may or may not develop in the next, and so on. A couple of examples may be given. Counting the internodes back from the apex, one never finds any trace of medullary vascular tissue in the first and second internodes (the apical meristem, being above the first node, is of course not counted). The central bundle normally develops in the third internode, and it may be developed in all of the nodes below this. An abnormal seedling of the ninth stage shows the bundle developed only in the seventh internode from the top, being entirely absent elsewhere. An abnormal seventeenth-stage seedling (near the end of the first growing season) shows the central bundle only in the third, fourth, fifth, seventh, eighth, twelfth, thirteenth, and fifteenth internodes.

Abnormalities in the peripheral bundles are less common. The failure of a side bundle to fork at the bottom of the internode has already been mentioned. In a single case of a mature seedling, another type of abnormality was found. In one of the basal internodes, the forks of one of the side bundles, undoubtedly normal in its younger state, had grown together at the base, owing to the large amount of secondary thickening. In the upper part of the internode there is a single bundle which forks normally, the forks coming together, however, at the base, the endodermis disappearing between them. As the leaf trace enters, the endodermis opens upon the outside and forms a complete sheath around the trace and the fused bundle, the latter opening just enough to allow the trace to be inserted between its halves.

In the basal internodes of the branches, there are usually four peripheral bundles. Rarely, however, one of the side bundles fails to be differentiated.

The mature plant

At the close of the growing season, the rhizomes produced at the base of the seedlings have developed the mature type of structure in their younger internodes. Growth now practically ceases, the

main axis of the seedling dying down. At the beginning of the next growing season, the growth of the plant is continued by the rhizomes, the apices of these turning upward as they grow, to form the aerial shoots, each internode of which contains one central and six peripheral bundles, each surrounded by a complete endodermis. The development of these internodal structures is exactly that which has been described for the seedling.

Passing back from the apex (see diagram, fig. 2), one finds at the second node a vascular ring, which just below the node breaks immediately into six bundles. As in the seedling, there is no differentiation of a sheath in this (second) internode. In the next node, however, a sheath appears, surrounding the vascular ring. Below this the sheath sinks in around the six peripheral bundles. An irregular sheath also appears around the central bundle, which first shows in this (third) internode. The internal endodermis passes through the next node in the manner already described in an old node of the seedling (figs. 3–8).

A cambium develops in the pair of bundles entering the stem from the leaves in the second internode from the apex. It appears in the side bundles in the next lower one. This cambium at first forms an incomplete ring, but in the older internodes it is frequently complete. The concentric structure thus produced, of pith surrounded by xylem, phloem, and a stereomatic pericycle, the whole surrounded by a sharply differentiated endodermis, certainly justifies HOLM'S statement (**5,** p. 309) that "in *Dianthera* the steles are very distinct and readily to be recognized as such, since they are cylindric and possess all the necessary elements."

The central bundle in the mature plant is plainly derived from vascular tissue passing downward from the four side bundles (figs. 2–7). As in the seedling, it arises first in the third internode, cambium usually showing in the fourth. The mature central bundle, as HOLM has described, usually has the appearance of being double, the mestome forming two arches, with parenchyma between, the whole surrounded by a well marked endodermal sheath.

The mature type of vascular structure seems to be rather constant. HOLM mentions that the central bundle may sometimes be lacking, but an examination of several hundred internodes of mature plants has failed to show such a condition. One single

internode, lying between two normal ones, showed three medullary bundles, the central one like the one ordinarily found, one a collateral bundle surrounded by an endodermis in structure therefore like one of the peripheral meristeles. The third, also surrounded by an endodermis, was a strictly concentric bundle, with no parenchymatous tissue, the protoxylem in the center, surrounded by a complete ring of xylem, cambium, and phloem.

The anastomosing of the bundles in the mature plant has already been described (fig. 1). Sections show that the minute vascular structure is very similar to that found in an old node of the seedling. Frequently, however, there is more of the inversely oriented vascular tissue. Some of the vascular elements on the sides of all six of the peripheral bundles may pass around to the inner face just before entering the node, and so become inverted.

HOLM, in speaking of the node, says (**5,** p. 323) "from the union of these steles each of the two opposite leaves receives three mestome cylinders, readily observed in the petiole as one central, very broad, and arch-shaped cylinder, with a much smaller one on either side." From the anastomosing bundles there is given off only one single trace to each of the leaves. This single trace, however, while passing through the cortex, gives off a branch on each side, so that each petiole does receive the three bundles as described by HOLM. This giving off of a single leaf trace, which trifurcates while yet in the cortex, is, according to VAN TIEGHEM (**11**), the conformation found in all of the Acanthaceae. It should be noted, however, that DEBARY (**3,** p. 243), in speaking of the course of the bundles in the stem, places *Ruellia maculata* in the group described as having "leaves opposite: traces of three or four bundles, which unite at the second lower node with those of the next lower pair: not pectinated."

The leaves of the aerial shoot have already been fully described by HOLM. In structure they are identical with those of the seedling, hence the correction concerning the presence of the marginal strand of collenchyma in the blade has to be made here also.

The axillary buds of the mature plant

As in the seedling, a bud is usually formed in the axil of each leaf. Those at the base of the aerial shoot usually develop into rhizomes, or more rarely into vertical aerial branches. In either

case, the development is exactly the same as in the buds of the seedling, having therefore an astelic structure. Each internode has six peripheral and one central bundle, except the basal, in which the central bundle may or may not be differentiated.

The buds of the upper part of the plant, on the other hand, ordinarily develop into inflorescence axes. As HOLM has pointed out, these have a monostelic structure (fig. 36). These buds start their development in the same way as do the buds which develop the rhizomes and stem branches. The first pair of leaves, or rather bracts, first furnish a pair of traces, then the pair of forked bundles develop; the second pair of bracts supply a pair of traces, exactly as in the other kind of bud. The connections of these bundles with each other and with those of the stem on which they are inserted are also as in the branch bud. The pedicel of the single flower developed in the axil of each bract possesses a ring of vascular tissue. At the base this ring splits on the face nearest the bract on one side, and nearest the inflorescence axis on the other. The two halves so produced become inserted between the bract trace and the forked bundle of the inflorescence axis.

The difference between the structure of the inflorescence axis buds and those forming ordinary branches soon becomes visible. One difference is the greater length of the internodes of the latter. The most important difference between them, however, lies in the fact that in the inflorescence axis, the inner layer of the cortex, while forming a rather irregular sheath around the stele, apparently never forms a strongly developed endodermis. This sheath, on passing out of a node, never sinks in between the bundles, but remains as a ring, marking the boundary, rather indistinct at times, between the cortex and the central cylinder. The parenchymatous tissue of the latter differs from that of the former in being made up of larger cells, and in containing a very much smaller proportion of air space. The general appearance of a cross-section is very similar to a monostelic stem in which the individual bundles tend to remain separate.

Let us now compare the insertion of a well developed branch with that of an inflorescence axis. Taking a case where the basal internode has no central bundle, we find that the trace of the subtending leaf enters between the abaxial side bundles of the branch.

The endodermal sheaths of the six branch bundles open up, each connecting with that of the adjacent bundles, so as to form a complete sheath around the leaf trace and the six branch bundles (figs. 33–35). Where the central bundle is present, a connection is made between the two pairs of side bundles and the central bundle, all of the vascular tissue of the latter passing to the periphery and becoming normally oriented. Then the ring of the six peripheral bundles and the incoming leaf trace become surrounded as before by a common sheath (figs. 37–41).

In the case of the inflorescence axis, the vascular ring shows a tendency to break up into six bundles. This ring opens on the side to allow the entrance of the leaf trace, or rather bract trace; the sheath then surrounds the ring and the trace (figs. 42–45). The structure so produced is in cross-section almost identical with that produced by the branch. The further history is the same for both types.

The organogeny of the flower

The apex of the inflorescence axis continues its activity all through the flowering season, giving rise to opposite, decussate bracts, in the axils of which are produced the flowers. The greatest growth of the inflorescence axis is due to intercalary activity in the basal internode.

In the axil of each developing bract a slight mound develops. On this mound, which is to be the flower, there appear first of all, apparently synchronously, the five sepals (fig. 46), followed very soon by the five petals. At first the latter are separate, but soon coalesce to form the corolla tube. About the same time that the corolla is initiated, two large mounds appear, marking the primordia of the stamens (figs. 47 and 48). There is never any trace of more than two stamens (five occur in some of the Acanthaceae, in other genera there are two stamens and three staminodia). The ovary grows up as a ring (fig. 49), the sides nearest and farthest from the axis of the plant being slightly (10–15 μ) higher (fig. 50). The petals soon coalesce, the stamens being carried up on the corolla tube. The ovarian "ring" closes in over the top and continues its growth to form the pistil with its deeply two-lobed stigma. The placentae grow out from the opposite walls of the ovary, near its base. Two ovules arise on each placenta. The two placentae now gradually

grow together, dividing the ovary into two cells. One ovule from each placenta is left in each cell.

The vascular supply of the floral organs

In the pedicel of a mature flower is to be found a complete ring of vascular tissue. Above this ring breaks up into 26 bundles, three of which pass out to each of the five sepals, five bundles passing up into the tube of the corolla, two large concentric bundles supply the stamens, and four pass up into the ovary. Two of the latter bundles, lying in the sagittal plane of the flower, pass up the carpellary walls, each giving off two laterals. The laterals die off near the top of the carpel, the medians however passing out into the style, which therefore possesses two bundles. The two remaining carpellary bundles branch, each giving off a bundle which supplies the placental wall. The other arm of each forks, the bundles so produced passing up the side walls of the carpel until near the top, where they disappear. Each of the five bundles passing out into the tube of the corolla gives off several branches while passing through the tube. Each of the stamen bundles pass up between two of the bundles of the corolla, being sharply distinguished from them in being concentric instead of collateral. They pass out into the stamens when the latter become free from the corolla tube.

As we pass down the short pedicel to its insertion, we find the ring first opens on the inner face (figs. 51 and 52). The inflorescence axis shows two large flat bundles, each of which now forks (figs. 51 and 52), each of the arms becoming applied to the sides of the opened ring from the pedicel (fig. 53). These two vascular masses then divide to allow the entrance of the single bract trace. The two vascular bundles now tend to round up (fig. 54). In the basal internode this division into two parts is not so marked, as the endodermal sheath usually forms a complete ring around the vascular tissue (fig. 36).

Discussion

According to HOLM, some of the species of *Dianthera* which he examined were monostelic. These were *D. comata* L., *D. glabra* B. & H., *D. inserta* Brandg., *D. ovata* Walt., *D. parvifolia* B. & H.,

D. pectoralis Murr., and *D. sessilis* Gray. I was unable to obtain any of these species for comparison. I did obtain seeds, however, of the fairly closely related *Justicia ventricosa*. A few of these germinated, and I was able to study a few of the seedling stages. The germination is similar to that described for *Dianthera americana*. Likewise are the first three stages. After that, the interfascicular cambium masks the primary structure.

Comparing this then with *Dianthera americana*, we find that they are at first exactly the same. The first point of difference is the failure of the interfascicular cambium to appear. This leaves the bundles separate, around which the endodermis turns in and surrounds, instead of remaining as a complete ring, as in *Justicia*.

In the mature plant, we find that the first two apical nodes of *Dianthera americana* are similar to other acanthaceous plants (*Justicia*, *Fittonia*, etc.). In the latter, the traces of the first pair of leaves pass down to a ring of vascular tissue. Below this node there are two arcs of tissue, each of which is evidently of three parts, showing three widely separated protoxylems. This internode, therefore, has a structure exactly like that of a young internode of the inflorescence axis of *Dianthera americana*. At the next node the opposite leaf traces enter between the two arcs. Below this node the original structure cannot well be made out, owing to secondary thickening.

It is evident that the seedling and the inflorescence axis of *Dianthera americana* show the primitive condition of the group, and that the formation of endodermal sheaths around each of the separate bundles, that is, the condition of astely, is a secondary condition, found only in a part of the species of *Dianthera* (according to Holm, *D. crassifolia* Chapm. and *D. lanceolata* Small, are also "polystelic").

Although astely apparently has not been previously described as occurring in the Acanthaceae, yet many other vascular abnormalities are known. The interxylary phloem of *Thunbergia* and others is well known. Intraxylary phloem (*Thunbergia*, *Hexacentris*, *Barleria*, etc.), medullary phloem (petiole of *Acanthus mollis*), and even medullary bundles (*Acanthus spinosus*, etc.), have also been described. It is thus seen that the family shows irregularities of vascular structure.

In *Dianthera americana*, the two chief types of abnormality found in the family occur, that is, the astelic condition and the medullary vascular tissue. The former is evidently not in any way dependent on the latter, since in the seedling the plant is frequently astelic when there is no medullary tissue developed.

In the terms of the stelar theory, *Dianthera americana* in its early stages is monostelic. In the young seedling the first endodermis differentiated, surrounding the nodal ring, corresponds to the inner layer of the cortex. The stem apex is rather broad and flat, but the three histogen layers of HANSTEIN can usually be made out. From the plerome is developed a central cylinder, all that is within the endodermis. The parenchyma of this stele corresponds, therefore, to pith and medullary rays.

This seems clear enough in the early stages of *Dianthera* and also in *Justicia*. In the latter this condition persists permanently; there is always a well marked cortex and central cylinder, with its pith. In the internode of *Dianthera americana*, on the other hand, an endodermal sheath about each bundle is initiated, passing around the bundle and inclosing on the inner face of the latter a mass of parenchyma. From our previous interpretation, this endodermis differentiates on the sides of the bundles from the parenchymatous cells of the medullary rays, and on the inner face from the pith itself. In such a case the endodermis surely cannot correspond with any morphological layer.

Now let us examine the fate of the parenchyma of the original central cylinder, that is, that derived from the plerome. That part which is inclosed within the endodermal sheath undergoes little change, while that outside the sheath gradually becomes so modified as to appear exactly the same as the cortical tissue. At this mature stage, then, there is no visible differentiation between the cortex and the pith, except within the endodermis. And yet we have seen that they had an entirely different origin, the one derived from the plerome, the other from the periblem. Unless one leaves out of account the different origin, and compares only the mature structures, one is certainly not justified in saying in this case, as VAN TIEGHEM and DULIOT (**12,** p. 275) say in their definition of astely, that the bundles are "directement plongés dans la masse

générale du corps qui ne se séparé pas alors en écorce et conjonctif" (p. 275).

STRASBURGER (9) distinguishes between the inner layer of the cortex, which is a morphological layer, and the endodermis, which is merely "an air-tight barrier which does not prevent the passage of water through its cells. Such a layer is found in a position to shut off the water-conducting system of a plant from its air-containing lacunar system, but this position may vary within the same genus, and has no necessary connection with any morphological region" (quotation from TANSLEY 10).

According to this interpretation of the endodermis, which is therefore merely a physiological layer, astely is merely a modification of monostely. This is the view already taken by STRASBURGER (9); the same idea is presented in a recent paper by GRÉGOIRE (4). The parenchyma of the central cylinder, that is, outside of the endodermis, becomes different from that inclosed within the sheath, owing to the different physiological environment, and it becomes, like the cortical tissue, a response to the same physiological conditions.

If we leave out of account for the present the surrounding endodermis, we see that the medullary system of *Dianthera americana* corresponds to what COL (1), in his work on the arrangement of bundles, calls "série M'." He defines this type as follows (p. 242): "faisceaux normaux rentrant dans la moelle de la tige. Ils s'accolent inférieurement à d'autres faisceaux medullaires, et tous ceux des entre-nœuds les plus inférieure de la tige se poursuivent et se terminent isolément dans la racine (dans le bois) ou à la base de la tige."

WEISS (14) has shown that all medullary bundles of the stem are foliar bundles. The work of LIGNIER (7), KRUCH (6), and COL (1, 2) fully confirms this. In *Dianthera americana* it is easy to follow the leaf trace downward through two internodes, and to see that a part then turns inward to form the medullary vascular tissue.

In a paper describing for the first time the medullary bundles of *Acanthus spinosus*, VESQUE (13) says that he thinks the primary effect of the internal position of the phloem is its very efficacious

protection. He calls attention to its common occurrence in lianes and in creeping plants, and says that the protection counterbalances the danger to the phloem due to the great length and weakness of the stem.

COL (**2**), on the other hand, presents the following hypothesis (translated from p. 275): "The histological structure of the conductive tissues does not permit a sufficient condensation to form a single circle. The wood becomes condensed, more easily than the phloem, into a small bundle; without doubt on account of the fluidity of the ascending sap, and of the easy passage of liquids from one vessel to another. For converse reasons, the phloem is less capable of becoming condensed." When two bundles come together, therefore, the phloem passes around the sides of the wood to the inner face, or it may even become medullary. While it is undoubtedly true that the phloem is better protected in its internal position, as suggested by VESQUE, yet from my observations on *Dianthera americana*, it would seem that the hypothesis of COL certainly holds in that plant.

It may be that, in this case, the internal vascular tissue is correlated with the lack of a complete ring of vascular tissue. The phloem, not finding sufficient room on the outer face of the individual bundles, becomes crowded around to the sides, or even to the inner face of the bundles. The new vascular tissue descending from the uppermost leaves does not find room for its insertion, so part of it at least passes inward to form the central bundle. After it has begun its development imbedded in the pith, a sheath finally differentiates to separate it from the air-containing tissue of the much modified mature pith.

As to the cause of the astelic conditions found in this and other species of *Dianthera*, very little can be said. It is probably correlated, however, with the aquatic habitat. The large amount of air space undoubtedly is to be correlated with the aquatic habitat. If we agree that the endodermis is not a morphological boundary, but a physiological layer separating the vascular tissue from the "air-containing lacunar system," as claimed by STRASBURGER, then we have a simple, plausible explanation of this phenomenon.

More comparative work on this and other species of *Dianthera*

is needed, however, especially to find out if possible the physiological value of the endodermis. Possibly such work would lead to the discovery of the reason why some species of this genus are monostelic, and apparently normal in every way, while other species are abnormal in being astelic, and in possessing medullary vascular tissue.

Summary

The mature plant of *Dianthera americana* is astelic, instead of polystelic, as claimed by HOLM. It possesses six peripheral meristeles and one central medullary bundle, each completely surrounded by an endodermal sheath. At the nodes these anastomose.

The seedling is at first monostelic; the individual bundles gradually become surrounded by the endodermal sheaths.

The mature type of structure with six bundles is derived from the seedling type with only four, by the increase of the size of the leaf gaps.

The inflorescence axis is monostelic.

Dianthera americana differs from related forms in the lack of interfascicular cambium, the individual bundles becoming surrounded by endodermis. Its medullary bundle is quite comparable to the medullary bundles of *Acanthus spinosus*, many Campanulaceae, and other plants.

It is probable that astely is merely a phase of monostely, the endodermis being a physiological layer, the medullary and cortical parenchyma becoming similar owing to like physiological conditions.

Astely in this plant is probably correlated with its aquatic habitat.

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EXPLANATION OF PLATES I–IV

All drawings of sections were made by means of a camera lucida. In the diagrams, xylem is represented by cross-hatching, phloem by dots. In figs. 3–9 the endodermis is represented by cells. The index letters are as follows: *A.R.*, adventitious root; *B*, bract; *BR*, branch; *BR.T.*, branch trace; *C*, carpel; *C.B.* central bundle; *CL*, calyx; *COT*, cotyledon; *CR*, corolla; *END*, endodermis; *EP*, epidermis; *ESP*, endosperm; *I.A.*, inflorescence axis; *L*, leaf; *L.T.*, leaf trace; *M.PH.*, medullary phloem; *P.B.* peripheral bundle; *PC*, procambium; *PPH*, protophloem; *P.R.*, primary root; *PX*, protoxylem; *S*, stamen; *ST*, stem; *T*, testa; *T.A.*, transverse arm.

PLATE I

FIG. 1.—Reconstruction of the vascular system of two adjacent mature nodes.

FIG. 2.—Diagram of the paths of the peripheral bundles of a mature stem.

FIGS. 3–8.—Series of successive transverse sections through a mature node, passing from fig. 3, made just at the top of the node, to fig. 8, made just below the node; ×45.

FIG. 9.—Transverse section through the upper part of an internode of an old seedling, showing one central and four peripheral bundles; ×45.

FIG. 10.—Part of a sagittal section of a seed, directly opposite the micropyle, showing the testa with its thickened epidermal cells, and the endosperm of two layers; ×185.

FIG. 11.—Sagittal section of a seed; ×12.5.

FIG. 12.—Longitudinal section of a seed, made perpendicular to the plane of the section shown in fig. 11, and through the line *mn;* ×12.5.

PLATE II

FIG. 13.—Transverse section of the upper part of the hypocotyl of a ripe seed, just below the insertion of the cotyledons; ×185.

FIG. 14.—Transverse section through the middle portion of the same hypocotyl, showing the periclinal division of the endodermis on either side of the stele; ×185.

FIG. 15.—Habit sketch of a seedling; stage I, with cotyledons still inclosed within the testa; ×1.5.

FIG. 16.—Transverse section of the upper portion of a first-stage seedling, just below the insertion of the cotyledons, showing the two "double" cotyledonary traces; ×185.

FIG. 17.—Diagram of the paths of the bundles in a seedling, stage I.

FIG. 18.—Diagram of the paths of the bundles in a seedling, early phase of stage II.

FIG. 19.—Habit sketch of a seedling, stage II (late phase); ×1.

FIG. 20.—Diagram of the paths of the bundles in a seedling, late phase of stage II.

FIG. 21.—Diagram of the paths of the bundles in a seedling, early phase of stage III.

FIG. 22.—Habit sketch of a seedling, stage III; ×1.

FIG. 23.—Transverse section of one of the side bundles in the basal epicotylar internode of a third-stage seedling, showing its "double" appearance, the three protoxylem, and three protophloem elements; ×380.

FIG. 24.—Transverse section of the same bundle as shown in fig. 23, at a lower level, just at the top of the fork; ×380.

FIG. 25.—Transverse section of the same bundle still lower down, the forking complete; ×380.

FIG. 26.—Surface view of a glandular hair; ×380.

FIG. 27.—Longitudinal section of a glandular hair and neighboring epidermis; ×380.

FIG. 28.—Transverse section of the uppermost internode of a third-stage seedling, showing the two procambial bundles of the traces of the uppermost pair of leaves imbedded in the ground meristem; ×380.

FIG. 29.—Diagram of the paths of the peripheral bundles in a seventeenth-stage seedling (near end of growing season), showing the gradual development of the "mature" type by the increase in length of the leaf gaps.

PLATE III

FIG. 30.—Restoration of the vascular system of a node of a fourth-stage seedling, showing the courses and attachments of the intranodal medullary phloem strands.

FIG. 31.—Habit sketch of an old seedling (stage XVII), near end of growing season, showing the development of rhizomes from the basal axillary buds; ×0.5.

FIG. 32.—Transverse section of the margin of the blade of a mature leaf, showing the collenchymatous strand; ×210.

FIGS. 33–35.—Series of successive transverse sections through the upper part of a node, showing the insertion of a branch which has no central bundle developed in its basal internode.

FIG. 36.—Transverse section of the stele of the basal internode of a mature inflorescence axis; ×45.

FIGS. 37–41.—Series of successive transverse sections through the upper part of a node, showing the insertion of a branch in which the central bundle has developed in the basal internode.

PLATE IV

FIGS. 42–45.—Series of successive transverse sections through the upper part of a node, showing the insertion of an inflorescence axis; ×50.

FIG. 46.—Longitudinal section through the apex of an inflorescence axis, showing the origin of the opposite bracts, the axillary flowers, and the primordia of the calyx on the lower flowers; ×50.

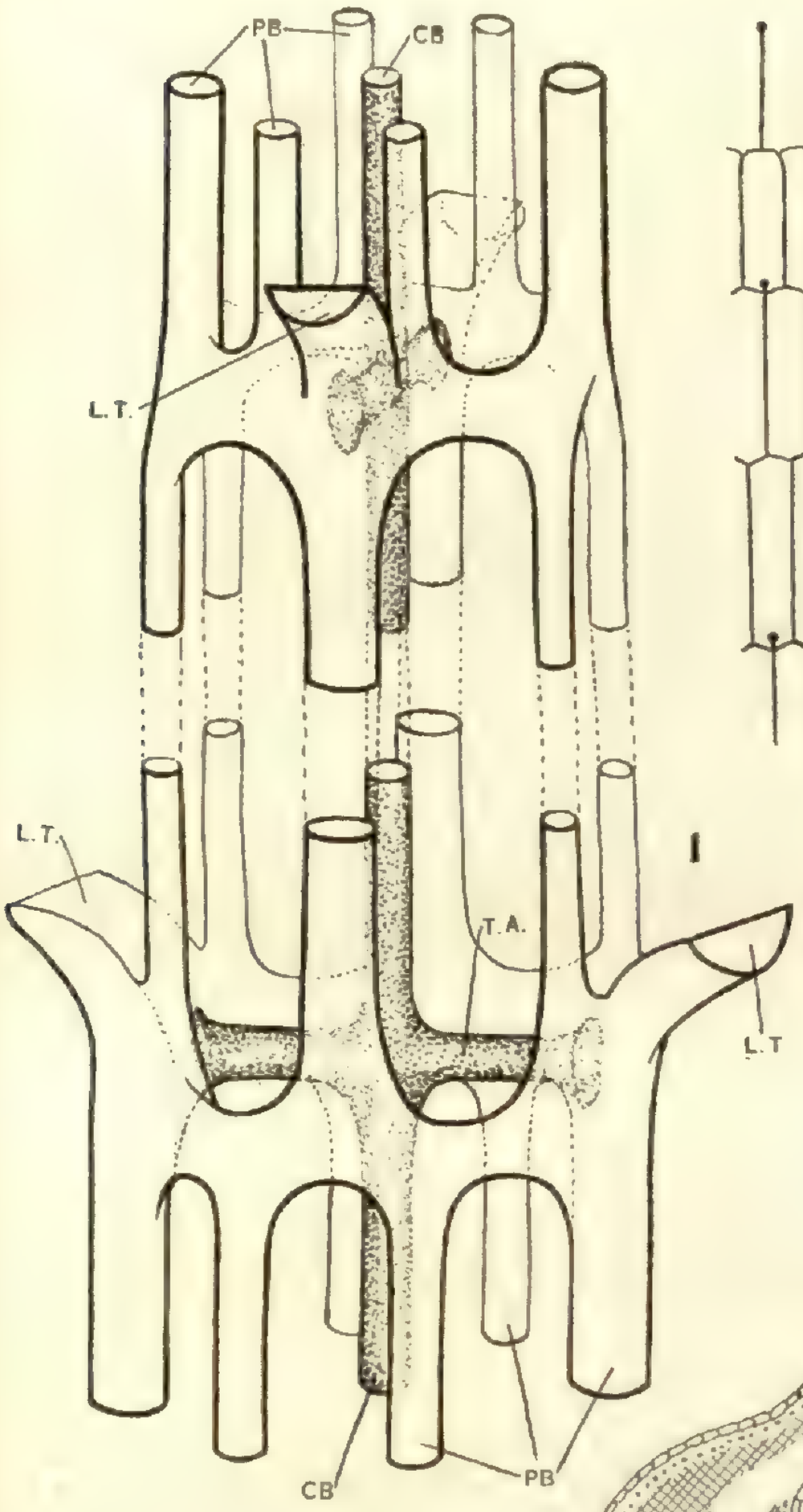
FIG. 47.—Longitudinal section of a young flower, not quite median, showing the bract, calyx, corolla, one of the stamens, and the edge of carpel; ×50.

FIG. 48.—Longitudinal section of a young flower, made perpendicular to that shown in fig. 47, along the line *mn*, showing the two large stamens free from the corolla; ×50.

FIG. 49.—Sagittal section of a slightly older flower, showing the formation of the ovarian cavity; ×50.

FIG. 50.—Transverse section (very slightly oblique) of a flower of about the same age as that shown in fig. 49, showing the arrangement of the floral parts, and the two lobes of the carpels; ×50.

FIGS. 51–54.—Series of successive transverse sections through a node of an inflorescence axis, showing the insertion of the bundles of the opposite pedicels and bracts with those of the main axis; ×22.5.



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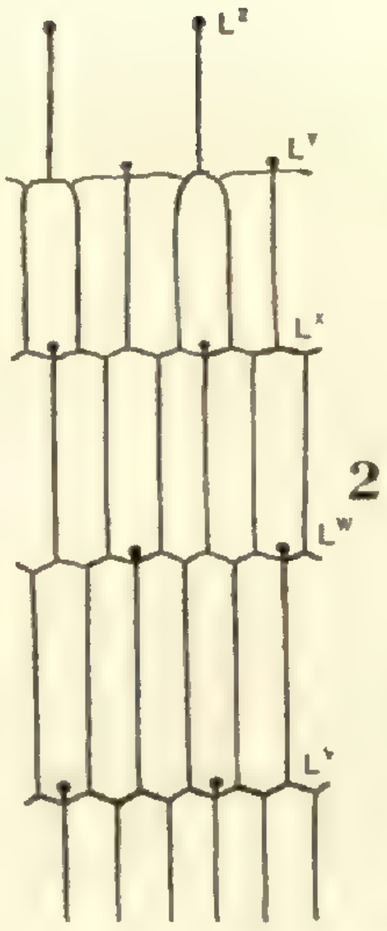

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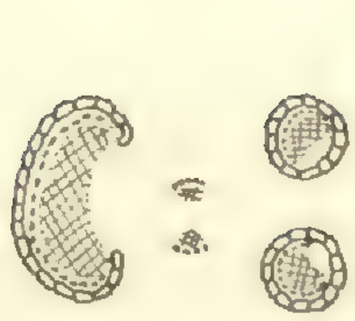
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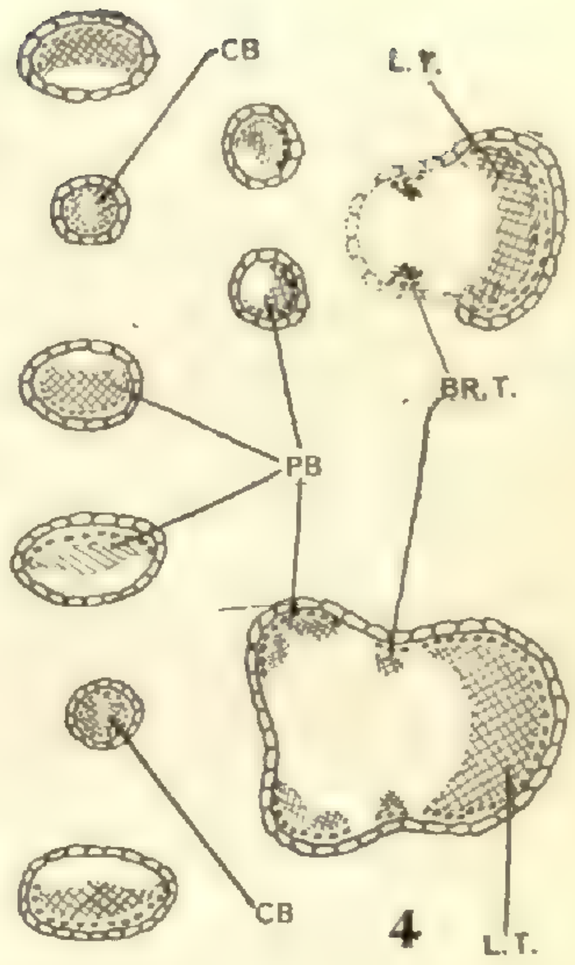

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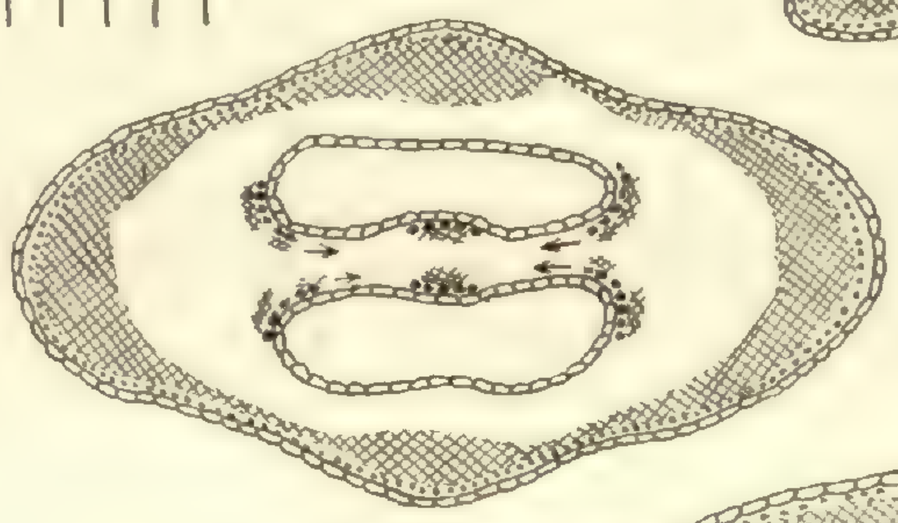
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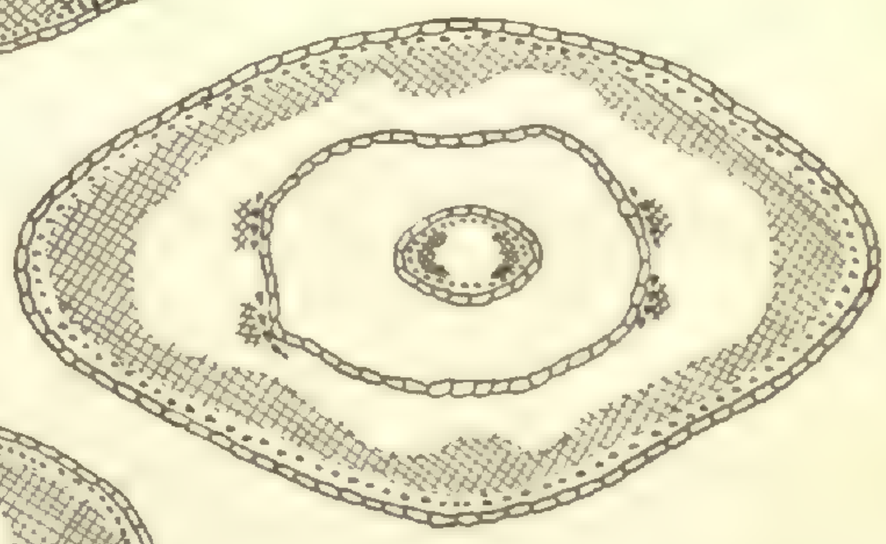
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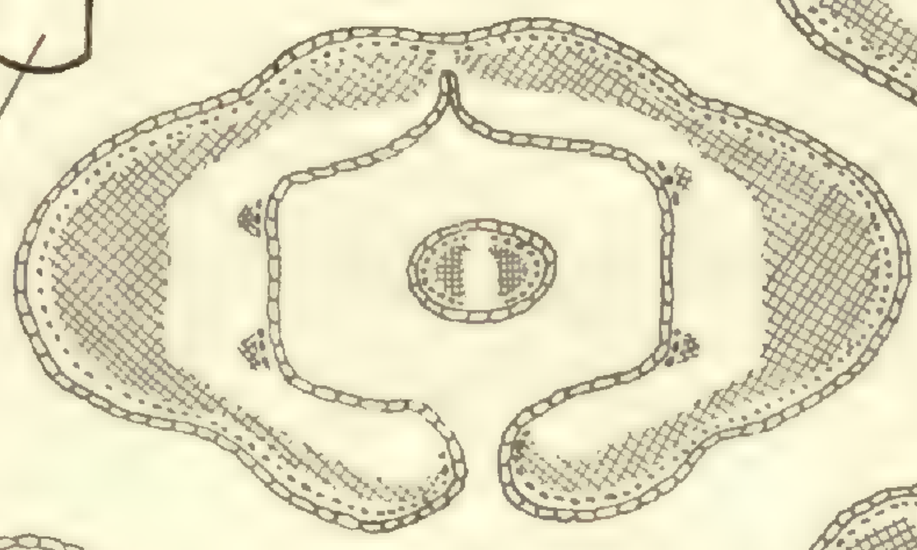
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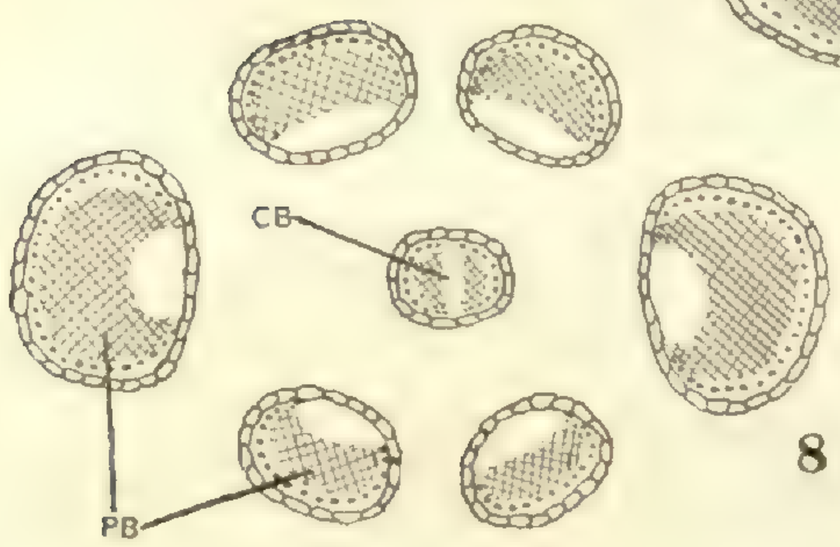

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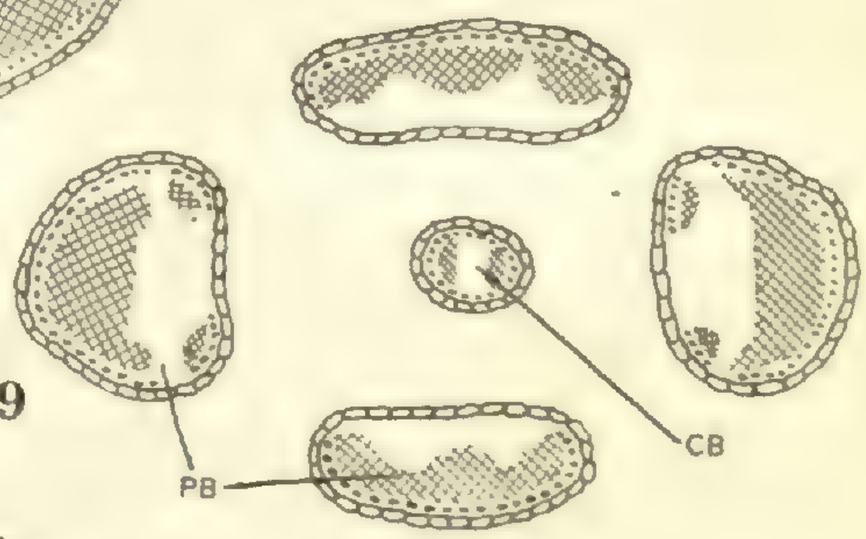

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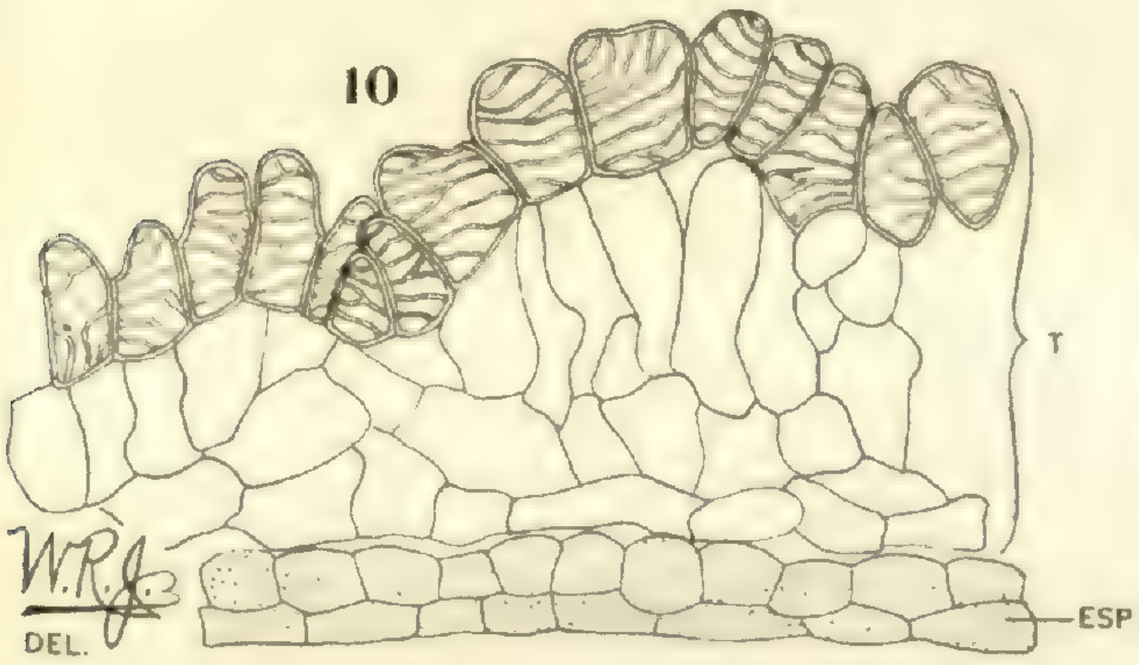

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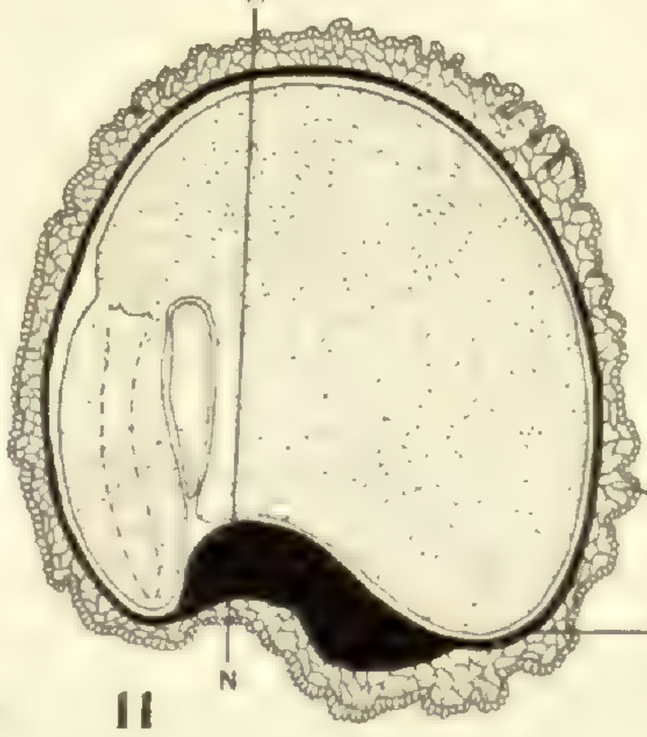

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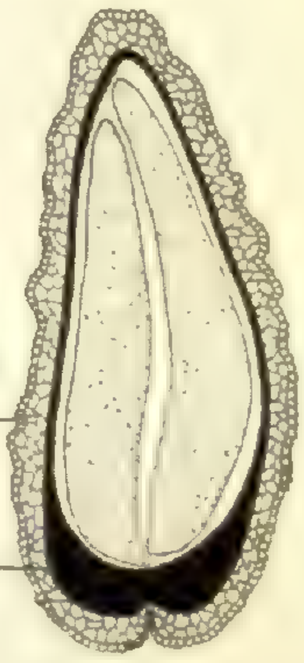
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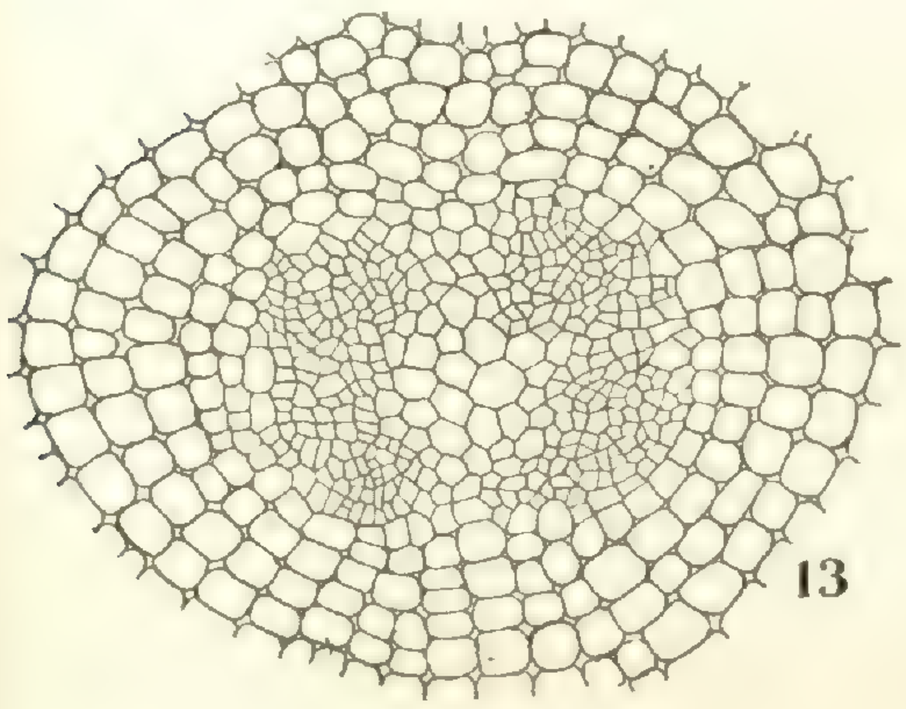

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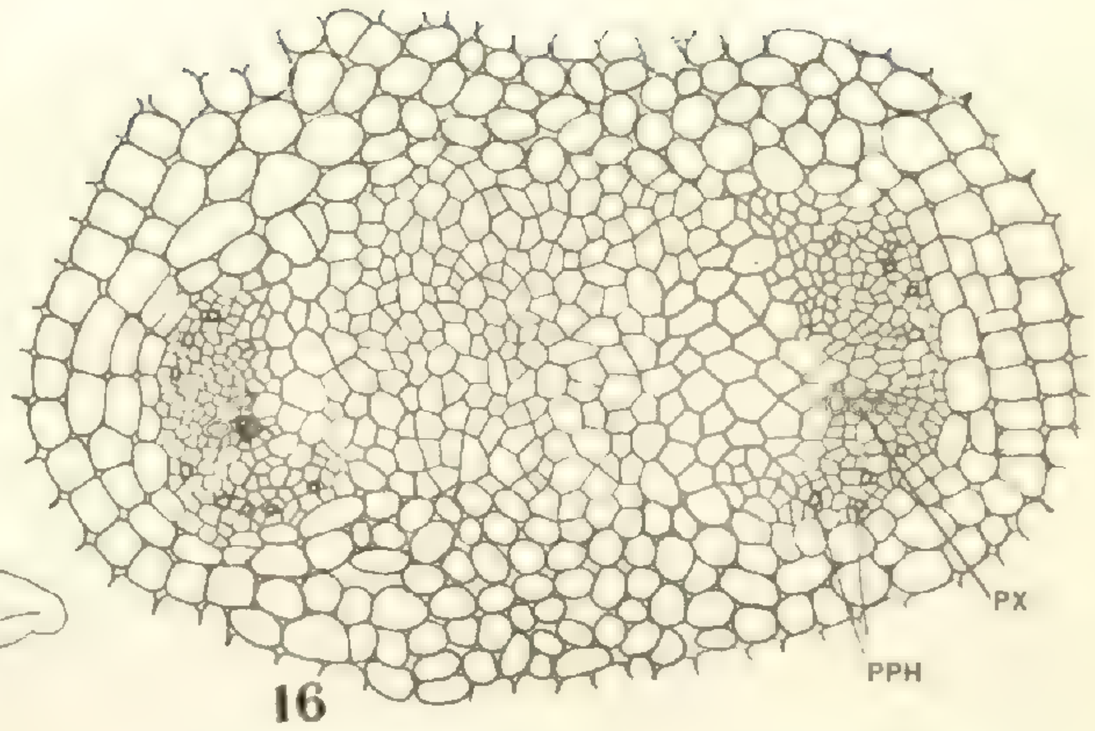

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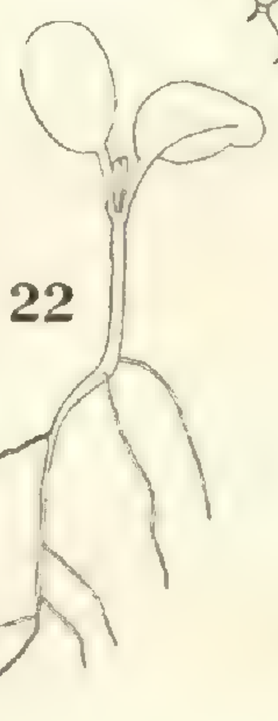

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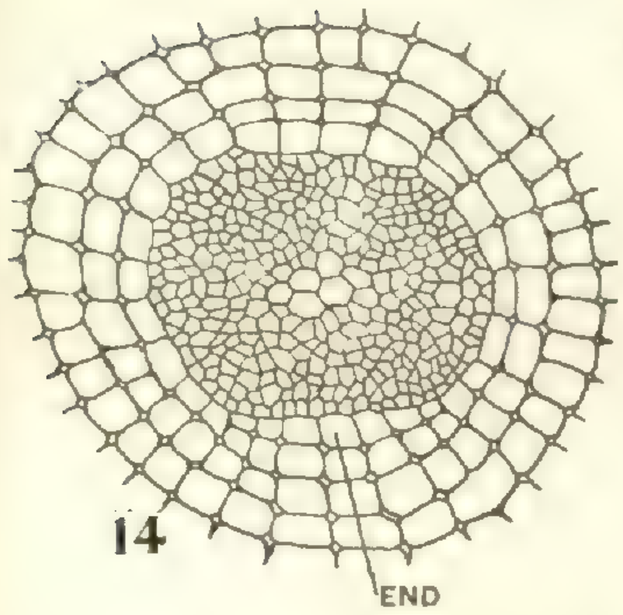

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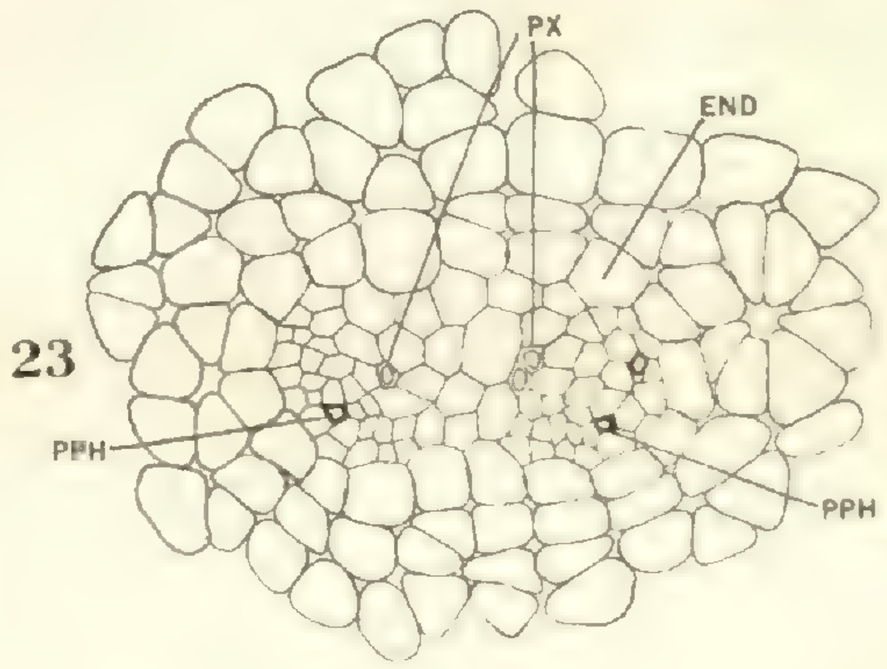

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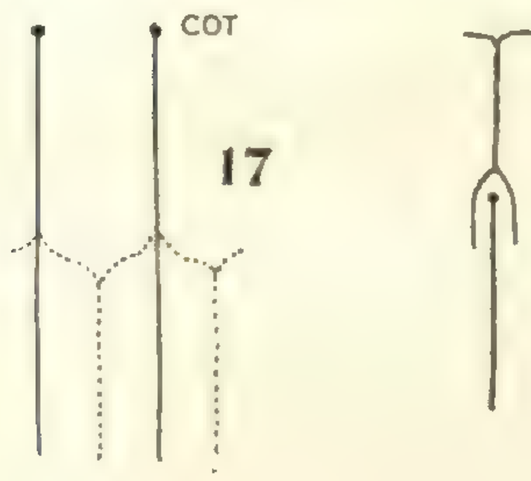

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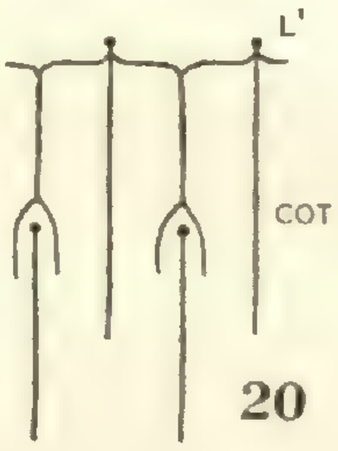

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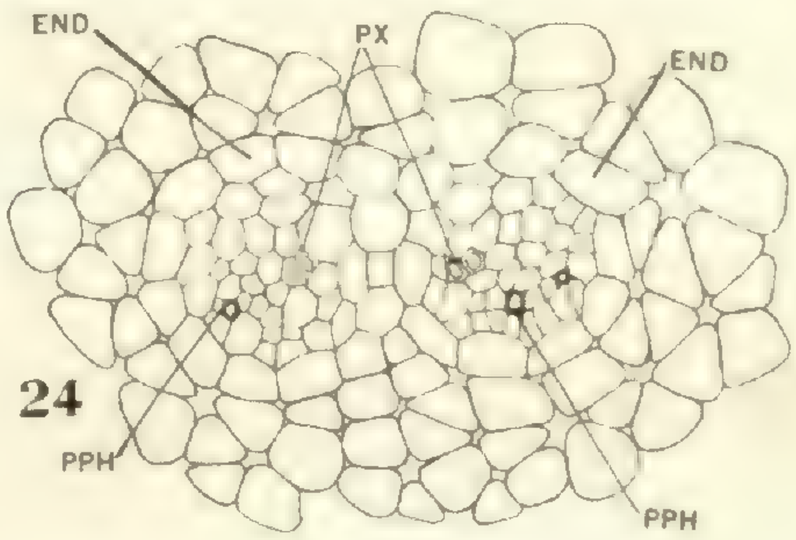

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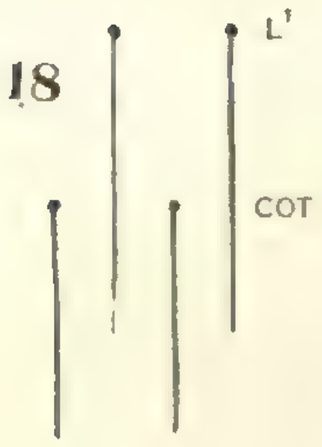

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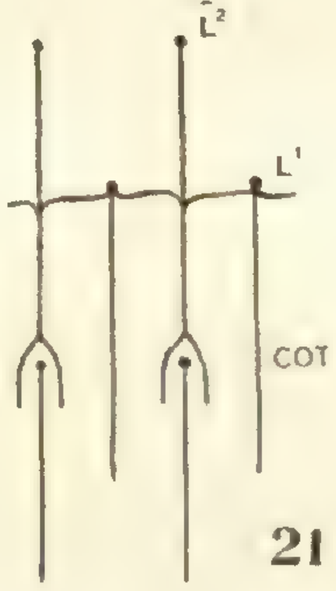

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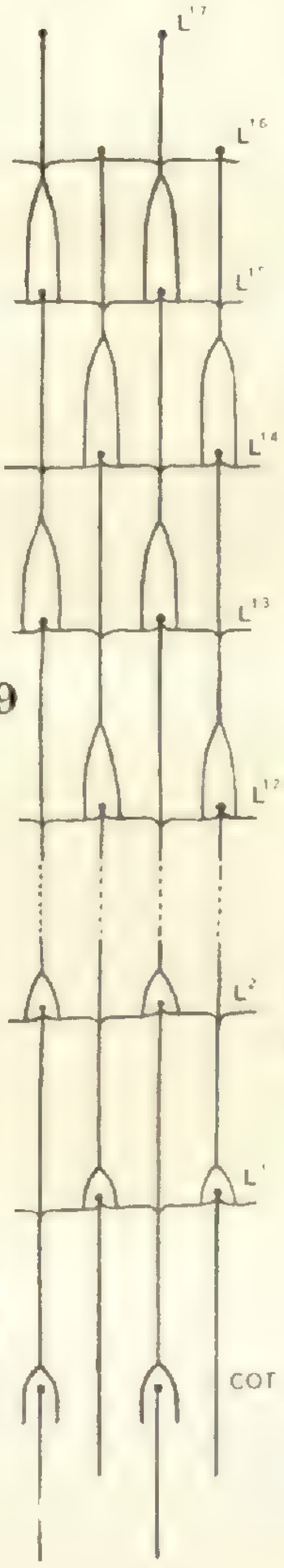

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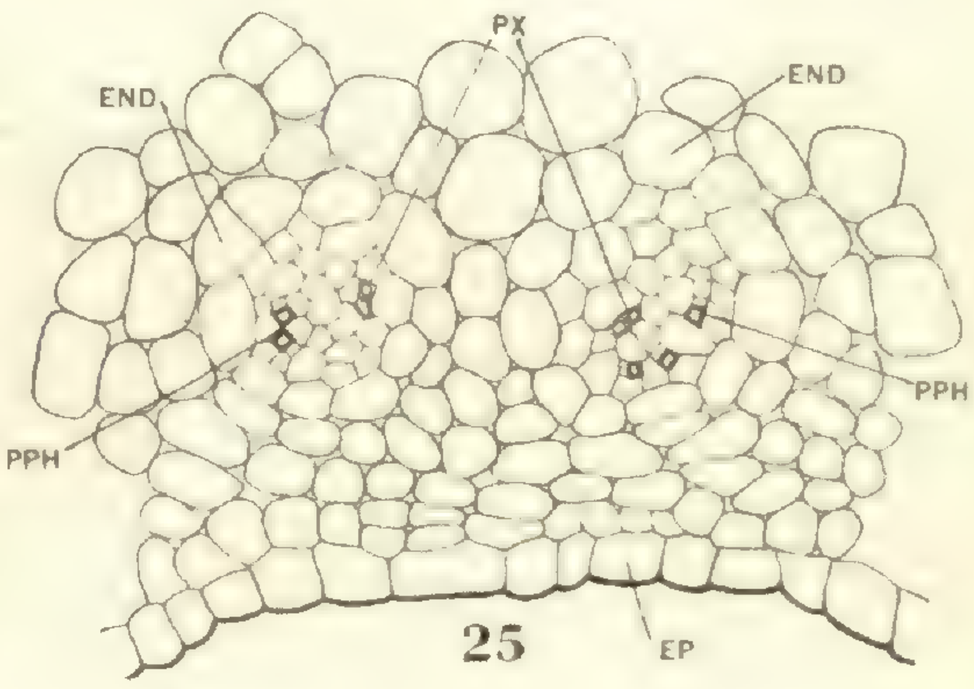

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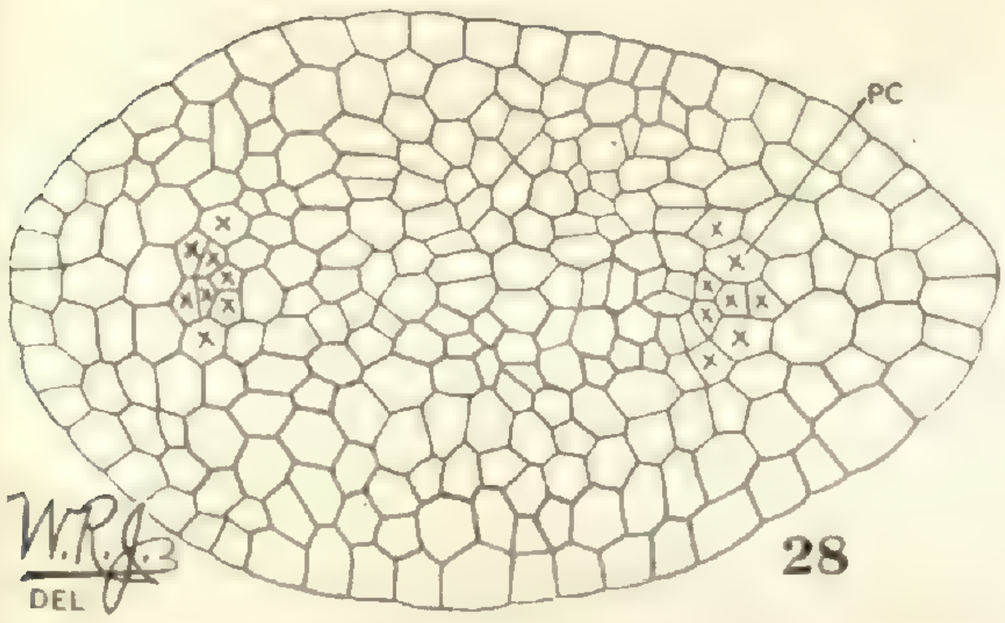

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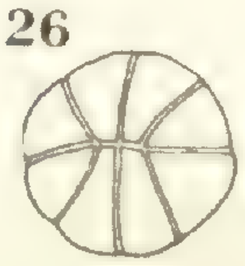

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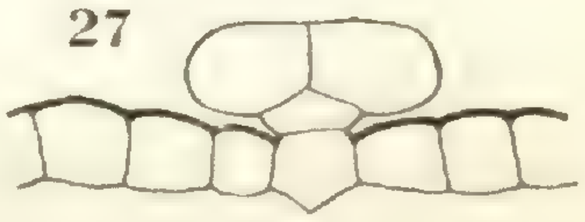

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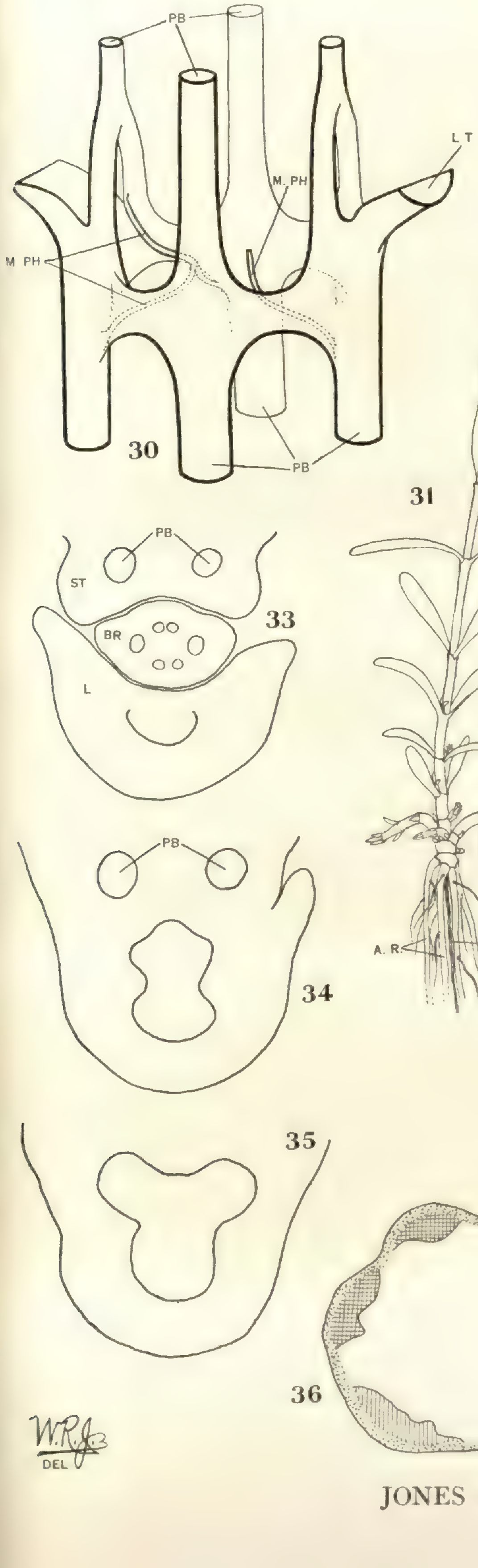

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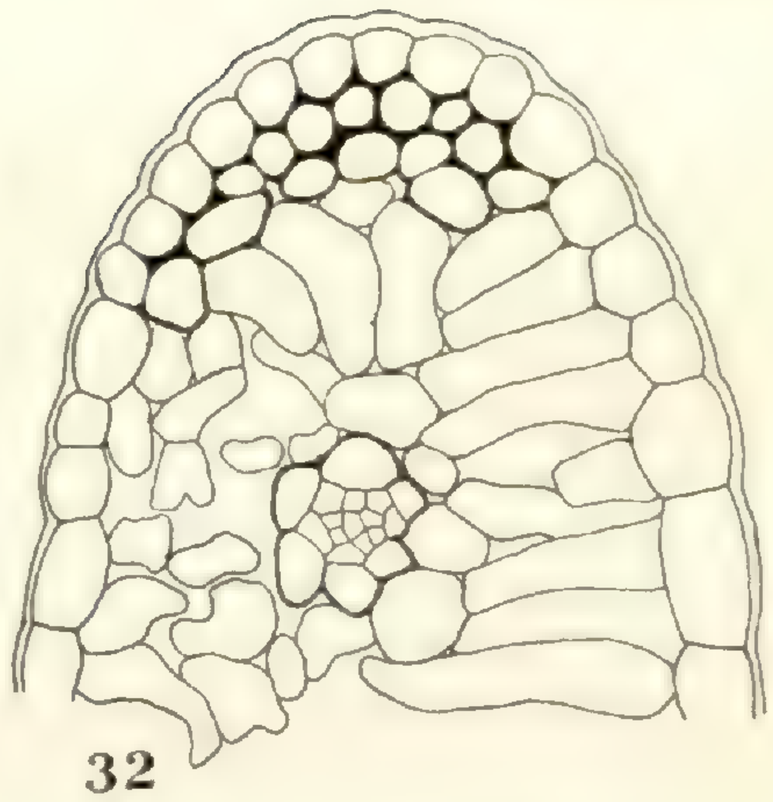

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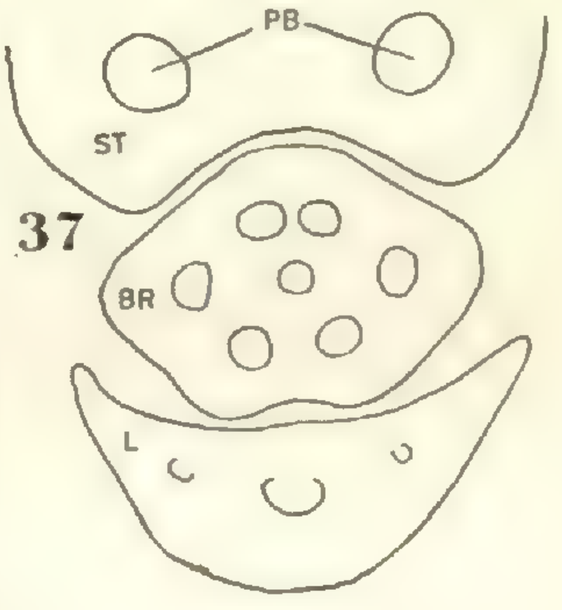

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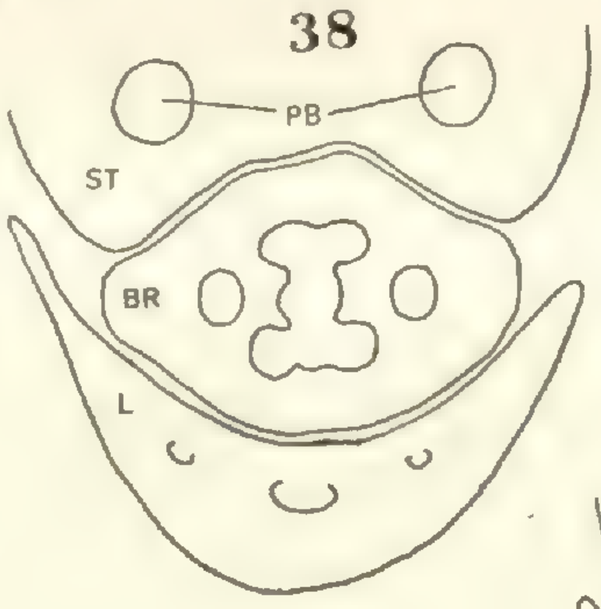

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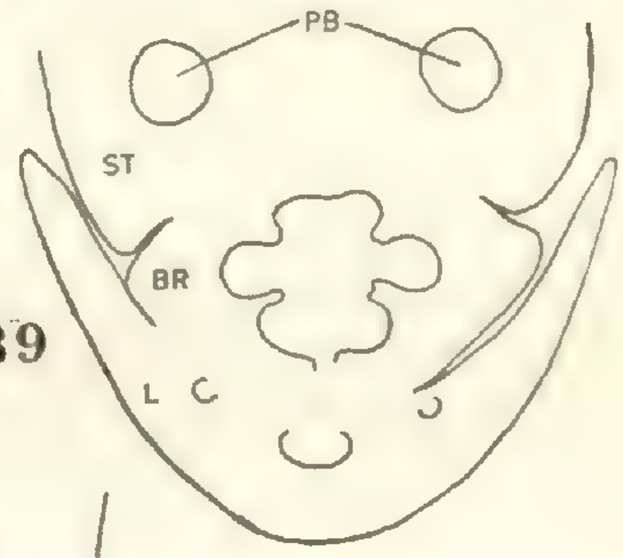

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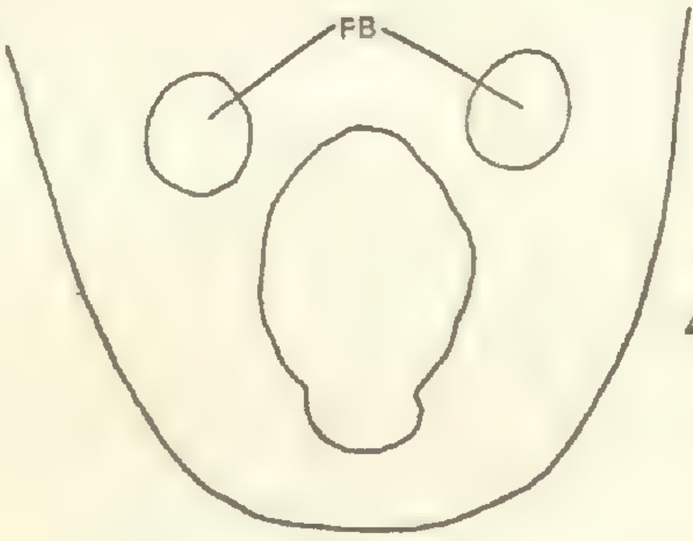

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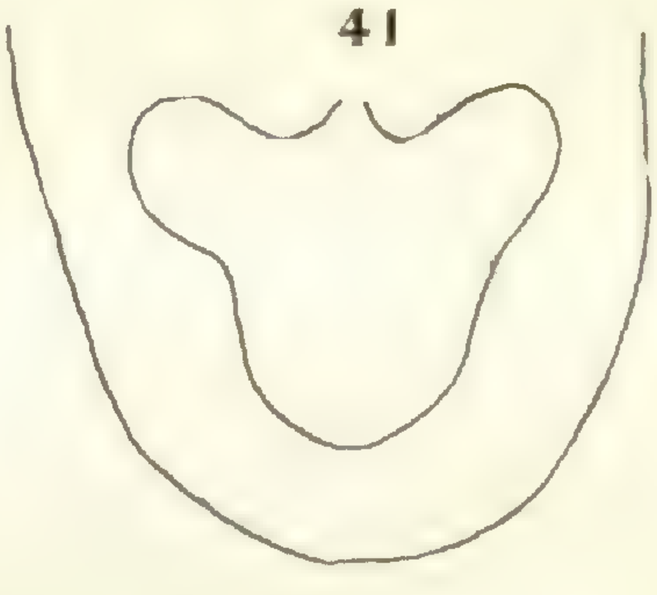

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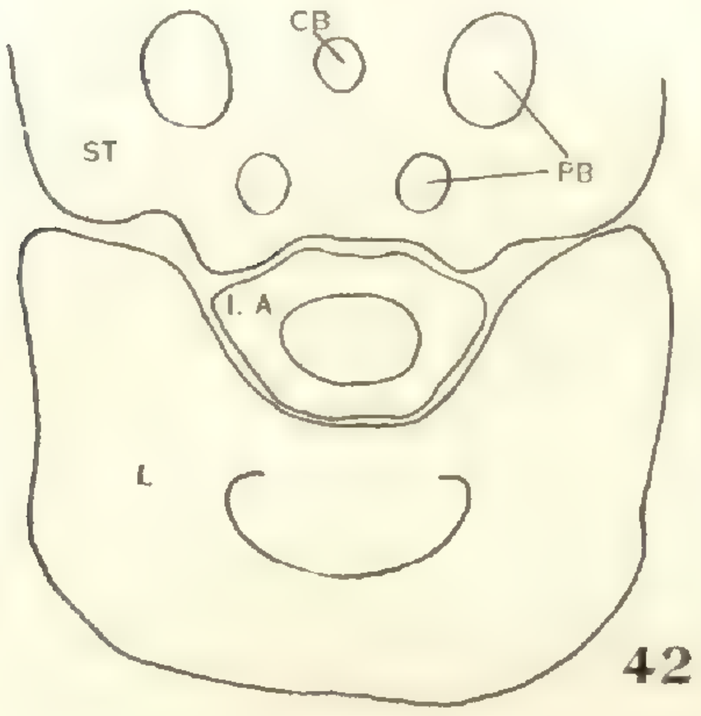
JONES on DIANTHERA



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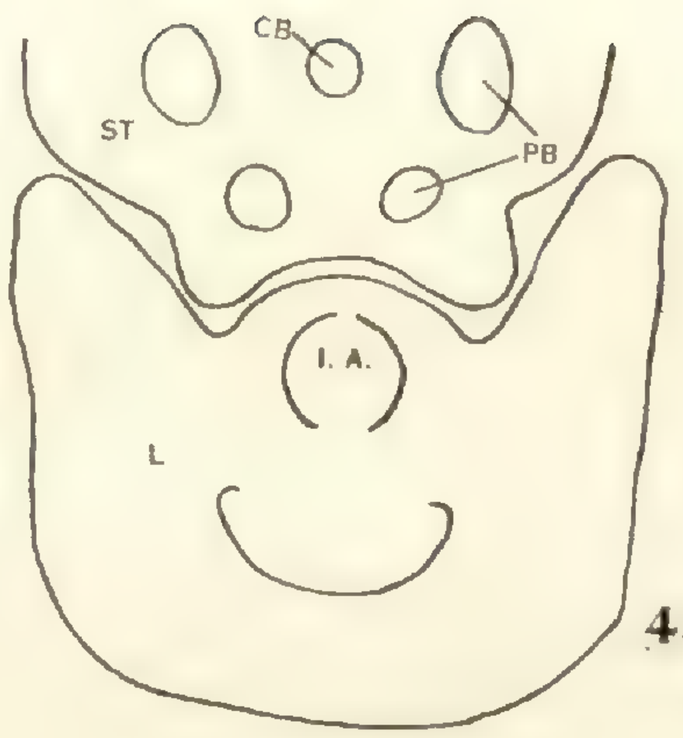

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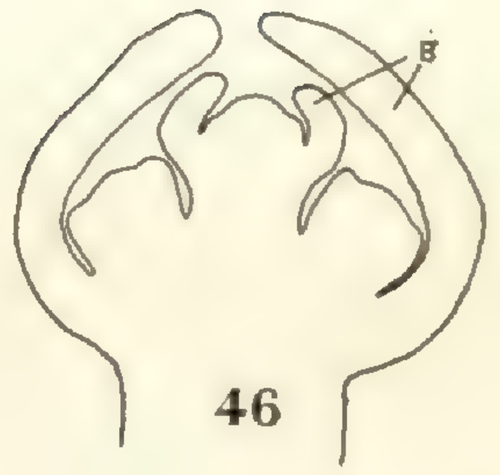

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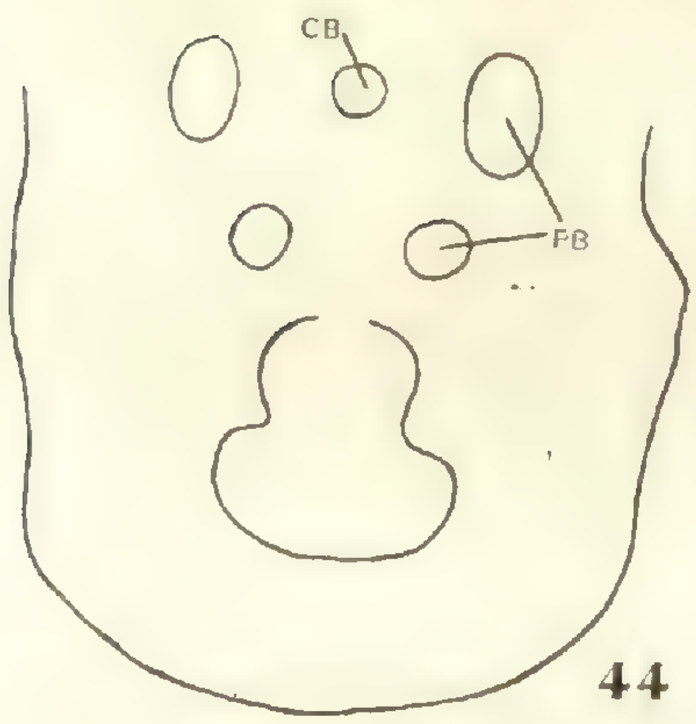

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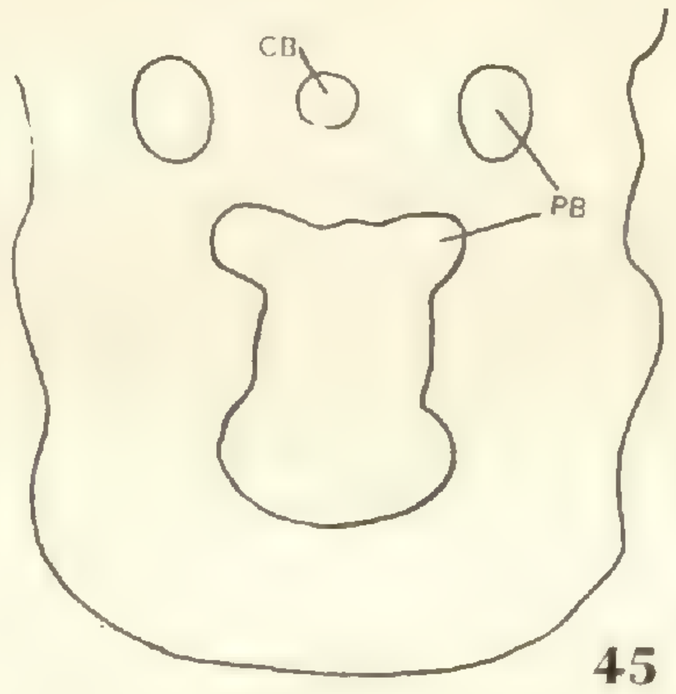

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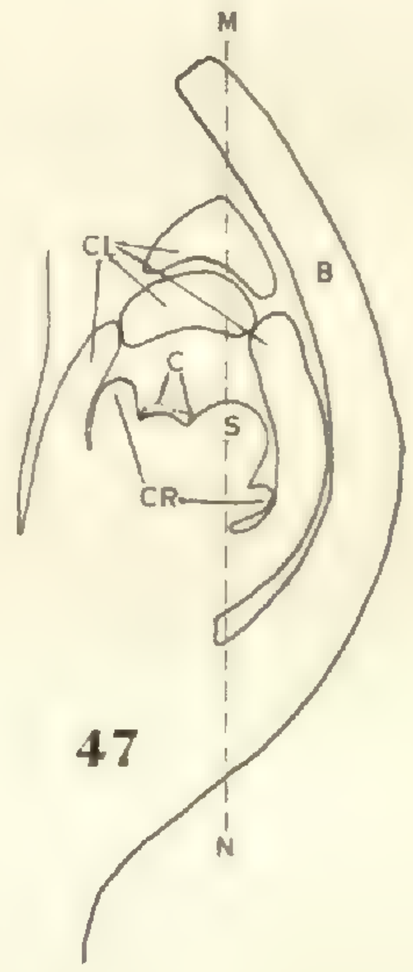

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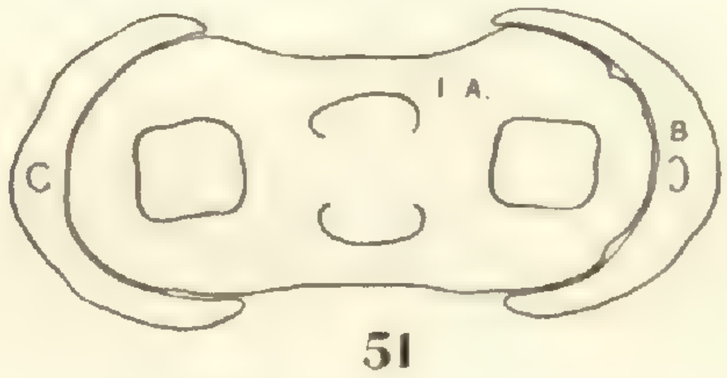

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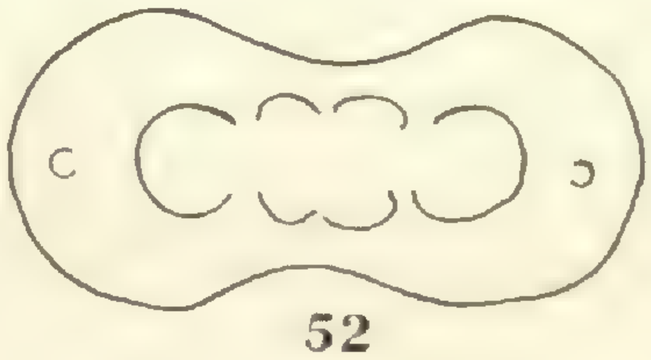

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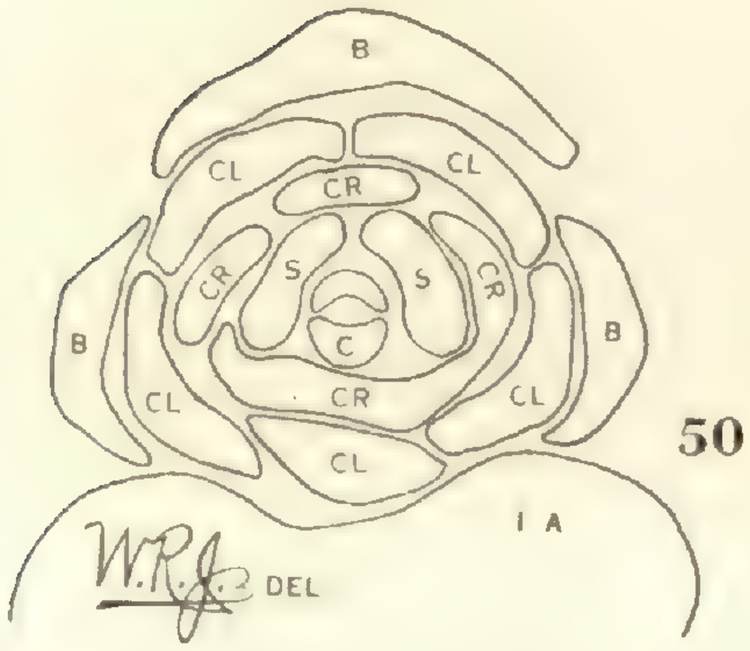

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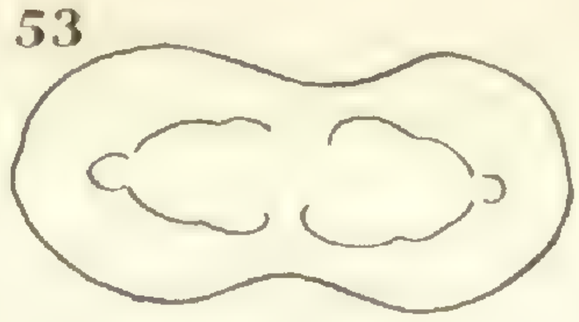

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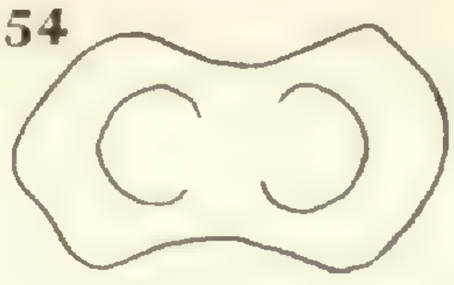

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JONES on DIANTHERA

THE TOXIC ACTION OF ORGANIC COMPOUNDS AS MODIFIED BY FERTILIZER SALTS[1]

OSWALD SCHREINER AND J. J. SKINNER

(WITH FIVE FIGURES)

In a former paper[2] the results obtained with dihydroxystearic acid, a crystalline organic compound isolated from a number of unproductive soils, was presented. The results obtained with this organic soil constituent, showing its effect on growth and absorption of plant nutrients from the various culture solutions containing a wide range of fertilizer composition, showed the desirability of obtaining further information concerning the behavior of other organic bodies known to be harmful to plants.

In the present paper some of the results obtained in experiments with toxic organic substances and the restraining influence on their toxicity by fertilizer mixtures of different composition will be given. The compounds studied, though not actually isolated from soil, are common constituents of plant débris, or result from this through changes, and so become, at least temporarily, components of the soil. The effects of a large number of such compounds on plant growth was given in an earlier paper.[3] Of these compounds, cumarin was selected for the continuation of these researches because it was quite harmful even in minute amounts, a few parts per million of solution having a noticeable effect on plant growth, and because it was a common constituent of a number of plants the remains of which get into the soil.

The earlier results were obtained in solutions of the cumarin in distilled water. The present investigation concerns itself with the effect of cumarin in the presence of nutrient salts as well, the

[1] Published by permission of the Secretary of Agriculture, from the Laboratory of Fertility Investigations.

[2] SCHREINER, O., and SKINNER, J. J., Some effects of a harmful organic soil constituent. BOT. GAZ. **50**:161. 1910.

[3] SCHREINER, O., and REED, H. S., The toxic action of certain organic plant constituents. BOT. GAZ. **45**:73, 271. 1908.

essential constituents of these being present to the extent of 80 ppm., but the composition varies. The number of culture solutions of the fertilizer salts used was 66, this being the number requisite to obtain every possible ratio of P_2O_5, NH_3, and K_2O, in 10 per cent stages. The system employed, as well as all details of preparation, was the same as already described in the similar investigation with dihydroxystearic acid already mentioned.

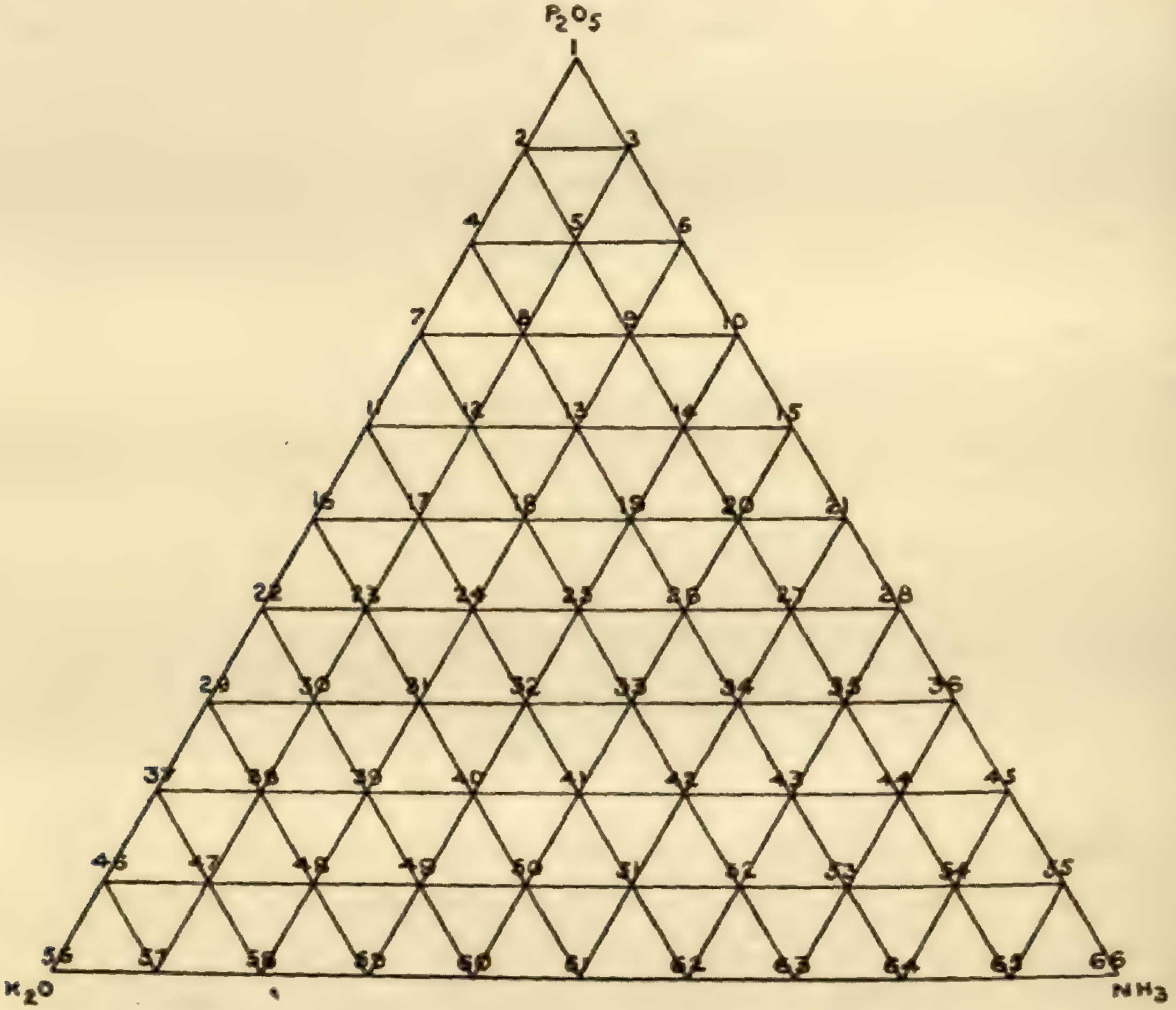

FIG. 1.—Showing the triangular diagram, with the points numbered, which represent the 66 culture solutions.

The triangular diagram is used as a guide. In this diagram (fig. 1), the apices, nos. 1, 56, and 66, are the cultures which contain only the single salts, calcium acid phosphate, sodium nitrate, and potassium sulphate, respectively; that is, the total of 80 ppm. contains 100 per cent of P_2O_5, NH_3, or K_2O, respectively. The line of cultures between 1 and 66 contains mixtures of P_2O_5 and NH_3 in 10 per cent differences; the line of cultures between 1 and 56

contains mixtures of P_2O_5 and K_2O in 10 per cent differences; the line of cultures between 56 and 66 contains mixtures of K_2O and NH_3. The cultures in the interior of the triangle contain mixtures of all constituents, differing in 10 per cent stages one from the other, the composition depending upon its position in the triangle; those nearer the P_2O_5 apex consisting chiefly of phosphate fertilizer, those nearer the NH_3 apex chiefly of nitrate fertilizer, and those nearer to the K_2O apex chiefly of potash fertilizer. For a more detailed explanation of the scheme and principles involved, the reader is referred to an earlier paper.[4]

Two sets of these 66 culture solutions were prepared, one of them containing in every culture 10 ppm. of cumarin. The total concentration of the nutrient elements $P_2O_5+NH_3+K_2O$ was in all cases 80 ppm. The culture solutions were contained in wide-mouth bottles and 10 wheat seedlings grown in each culture after the manner described in the paper cited. The culture solutions were changed every three days, four such changes being made in each experiment. The culture solutions were analyzed immediately after each change for nitrates, but the phosphate and potassium were determined on a composite of the four changes. The green weight of the plants was determined at the termination of the experiment. The first experiment with cumarin was set up on December 9 and discontinued December 21.

The effect of even so low a concentration as 10 ppm. of cumarin was strikingly noticeable in the difference between the plants growing in the two sets of cultures. The appearance of plants growing in solutions containing cumarin is very characteristic and totally different from the effect on wheat of any other toxic compound worked with in this laboratory. The leaves are shorter and broader than is normal for wheat, and only the first leaves are usually unfolded, the other leaves remaining wholly or partially within the swollen sheath; such leaves as do break forth are usually distorted and curled or twisted. The appearance is so characteristic that the investigator can pick out the cumarin-affected plants from those affected by any other toxic body in the same experiment by

[4] SCHREINER, O., and SKINNER, J. J., Ratio of phosphate, nitrate, and potassium on absorption and growth. BOT. GAZ. **50**:1. 1910.

a mere glance. This characteristic behavior of cumarin-affected plants becomes, therefore, in addition to the usual criteria, an indicator of the degree of its harmfulness in the cultures of different composition in this experiment. In addition to its effect on the tops, as just described, there was a general inhibition of root growth, as is the case with many other substances, notably the dihydroxystearic acid already described.

The effect of the cumarin was to depress the green weight of the plants from 100 to 88 as an average in this experiment, although it was obvious from the appearance of the cultures that its effect was far from uniform in all of the cultures, and this is the most interesting feature of the experiment.

It will be recalled that with dihydroxystearic acid the more normal growth was observed in the nitrogen end of the triangle, but when the cumarin cultures were set out in this triangular form according to the composition of the culture solutions, it became at once apparent that the result with the cumarin was not in harmony with the observation so repeatedly made with the dihydroxystearic acid. It was clear that the cumarin had an entirely different effect in the different culture solutions from that observed in the case of dihydroxystearic acid, which had responded most in the fertilizer combinations high in nitrate. With the cumarin the growth was more nearly normal in the fertilizer combinations high in phosphate. In comparing the cultures, those of like composition only are compared in the cumarin and in the normal sets.

This influence of the phosphate on the harmful effect of the cumarin is perhaps most strikingly shown in the difference between the plants growing in the culture solution containing no phosphate whatever, namely along the line 56 to 66 in fig. 1, and the line of cultures immediately above this, containing 10 per cent phosphate in the fertilizer mixture. Where phosphate is entirely absent, the effect of the cumarin is most marked. Above this line the harmful effect of the cumarin steadily decreases, and in the upper part of the triangle disappears altogether, so far as the eye can detect this in the appearance of the plants in the normal and cumarin set.

The effect of the phosphate in overcoming the harmful action

of the cumarin is shown in the green weight of the plants taken at the termination of the experiment. In table I is given the green weight of the series of cultures containing the same amount of phosphate; that is, the series along any one of the horizontal lines in fig. 1.

TABLE I

SHOWING THE INFLUENCE OF PHOSPHATE IN OVERCOMING THE HARMFUL EFFECT OF CUMARIN

PERCENTAGE OF P_2O_5 IN FERTILIZER MIXTURES	PARTS PER MILLION OF P_2O_5 IN ORIGINAL SOLUTIONS	NUMBER OF CULTURES INCLUDED	GREEN WEIGHT OF CULTURES		
			Without cumarin	With cumarin	Relative (without cumarin = 100)
0	0	11	21.773	15.370	70
10	8	10	22.408	18.835	84
20	16	9	20.339	17.140	84
30	24	8	17.143	15.350	90
40	32	7	15.008	14.085	94
50	40	6	11.188	11.150	100
60	48	5	9.113	9.005	99
70	56	4	6.915	6.485	94
80	64	3	4.171	4.330	104
90	72	2	2.388	2.530	106
100	80	1	0.932	0.955	102

The last column of the table gives the relative growth between the two sets of cultures, with and without cumarin. It will be seen from the last column of the table that in those cultures in which no phosphate was present the depression in growth caused by cumarin was greatest, being reduced to 70 per cent of the normal, and that the introduction of 8 ppm. of phosphate caused the growth to rise to 84 per cent of the normal. On further increasing the phosphate content to 16, 24, 32, and 40 ppm., the green weight rose to 84, 90, 94, and 100 per cent of the normal, respectively. From this point on the growth is practically as good in the cumarin set as in the normal control set, thus showing that, on the whole, the fertilizer combinations high in phosphate were practically able to overcome the harmful influence of the toxic cumarin.

The lessened toxicity of cumarin in solutions high in phosphate is also shown when the results of the experiment are grouped in such a way as to obtain all cultures containing 50 per cent and over of any one of the three constituents, P_2O_5, NH_3, and K_2O, as was

done in the case of the dihydroxystearic acid experiment. This is accomplished by taking the cultures contained in the smaller triangles formed at each angle of the larger one shown in fig. 1; that is, the cultures contained within the triangles 1, 16, 21; 21, 61, 66; and 16, 56, 61, respectively. The sum of the green weights in these respective triangles is shown in fig. 2 for the normal and the cumarin sets, together with the relative growth. The phosphate

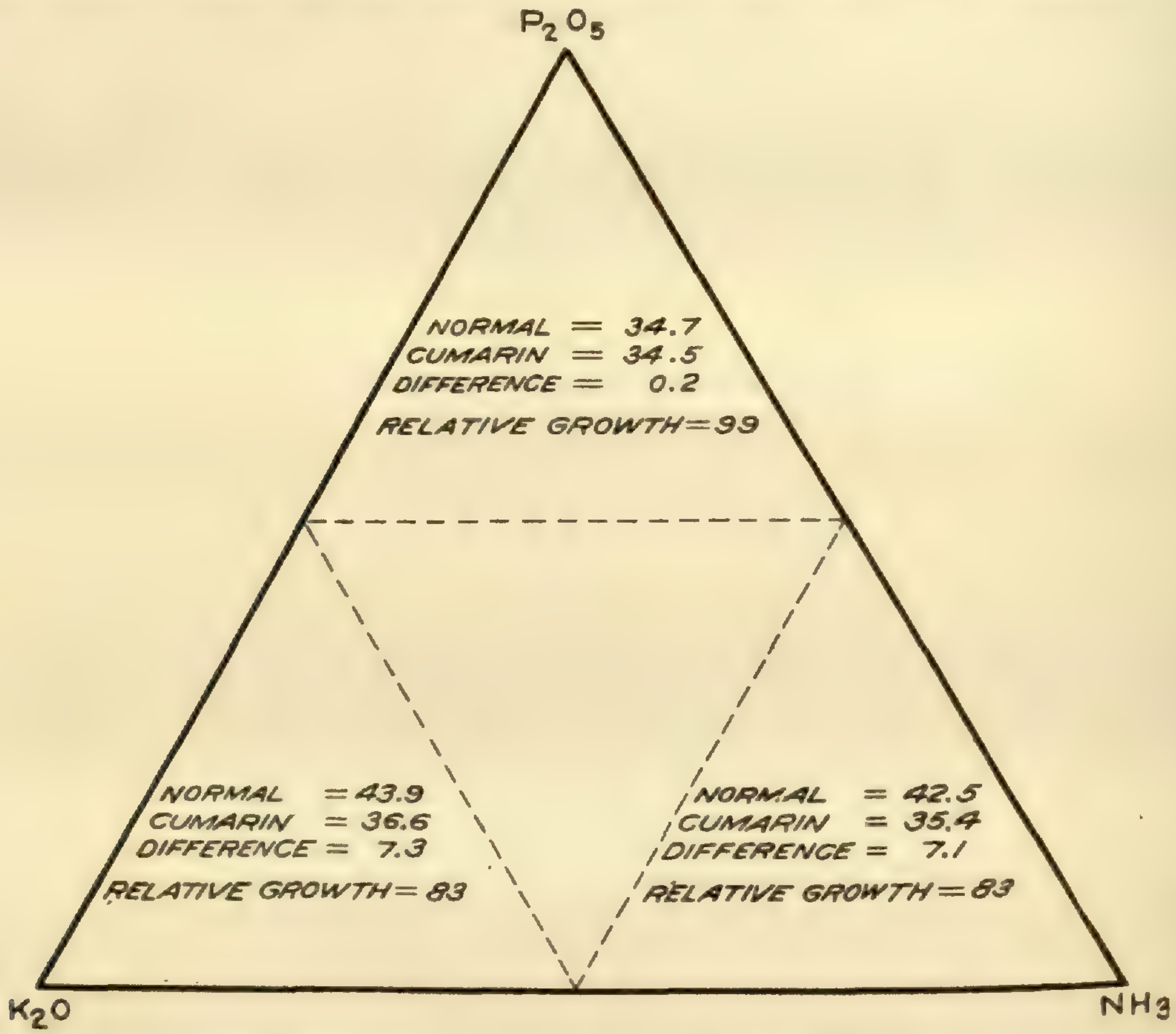

FIG. 2.—Showing the relative growth of normal and cumarin cultures in solutions high in phosphate, nitrate, or potash, respectively.

end shows that the growth in the cumarin set was nearly normal 99 per cent, whereas the potash and the nitrogen end showed a growth only 83 per cent of the normal.

A second set of experiments with cumarin was made and was in all respects conducted as in the first experiment. This grew from January 12 to January 24.

The cumarin-affected plants showed the same characteristic stunting of the leaves as in the former experiment, and, moreover,

again showed strikingly the influence of phosphate in overcoming this effect, the general appearance of the entire triangle of cultures being similar to that already described. The effect of the cumarin was to depress the green weight from 100 to 75 in this second experiment, this being the average depression for all the cultures in the set. Here, as in the first experiment, the toxicity of the cumarin was lessened most in the solutions high in phosphate, being 85 per cent of the normal as compared with 74 and 70 per cent in the cultures high in nitrate and potash, respectively.

The line of cultures containing no phosphate whatsoever again showed the greatest effect of the cumarin; this harmful influence becoming less and less until complete recovery of the plants is noticed in the cultures containing higher amounts of phosphate. The total absence of phosphate showed a depressed growth equal to 62 per cent of the normal; this rises to 70 per cent on the addition of 8 ppm., and to 76 per cent on the addition of 16 ppm., and so on upward, somewhat irregularly but definitely, until in the higher concentration of phosphate the effect of the cumarin is lost entirely.

The foregoing experiments show clearly the influence of cumarin on growth and the effect of phosphate in counteracting the harmful influence of the cumarin. There remains to be considered the influence of the cumarin on the concentration of the solution during the growth of the plant.

Mention has already been made of the fact that the concentration differences produced by the growth of the plants in the various cultures was determined by making an analysis for nitrate at the termination of every three-day change, and of the phosphate and potassium on a composite of the solutions from the four changes. It is thus possible to compare the results obtained under the so-called normal conditions without the cumarin and under the conditions where 10 ppm. of cumarin were present in the solution. The 36 cultures comprising the fertilizer combinations in which all three fertilizer elements are present were consistently analyzed and these only are here considered.

The amount of total $P_2O_5+NH_3+K_2O$ removed from solution by the growing plants in the total number of 36 cultures was 1379 milligrams under the normal conditions and 1272 milligrams in

the cumarin set. In table II are given the results for the P_2O_5, NH_3, and K_2O, separately, under the normal conditions and in the cumarin set.

TABLE II

TOTAL MILLIGRAMS OF P_2O_5, NH_3, AND K_2O REMOVED FROM THE 36 CULTURE SOLUTIONS CONTAINING ALL THREE OF THESE INGREDIENTS

	TOTAL ABSORPTION IN MILLIGRAMS		RELATIVE	PERCENTAGE OF CUMARIN CULTURES ABOVE NORMAL
	Normal	Cumarin		
P_2O_5	278.5	264.5	95	57
NH_3	482.6	415.3	86	22
K_2O	618.2	592.6	96	39

An examination of these figures discloses the fact at once that while the cumarin has decreased the absorption of these nutrient elements, it has not decreased it anywhere near the extent shown by dihydroxystearic acid in the experiment cited. The third column of figures gives the relative effect of cumarin absorption of each nutrient element, and indicates that the phosphate and potash absorptions were the more nearly normal of the three, especially the phosphate absorption if the figures in the last column are taken into account. This column gives the percentages of the individual cumarin cultures which showed an absorption equal to or greater than the corresponding culture without cumarin.

In the second experiment this effect is clearly marked, the phosphate absorption being 91 per cent of the normal, as compared with 78 and 87 for the nitrate and potash, respectively. In this experiment the total absorption of $P_2O_5+NH_3+K_2O$ was 1267 milligrams under normal conditions and 1077 milligrams with cumarin.

While these figures indicate a somewhat more normal phosphate absorption in the cumarin set than normal nitrate or normal potash absorption, the figures are, nevertheless, not decisive enough to enable one to say definitely that the antagonism of the phosphate to cumarin, as shown in the growth of the plants, is due to this cause alone. A rigid examination of the complete data does not allow us to draw this conclusion without at the same time suggesting the possibility of an external interaction between the lactone

cumarin and the acid calcium phosphate. The possible solutions of the problem must be left for future investigation.

From the foregoing results it is apparent that the two toxic substances studied, dihydroxystearic acid and cumarin, show markedly different physiological properties, and are very differently influenced by fertilizer salts. Whether this is a direct action of the fertilizer on the organic body or through the medium of the plant cells, making the toxic substance and the particular fertilizer salt physiologically antagonistic, cannot be definitely stated.

The cumarin so affected the normal development of the wheat as to cause stunting of leaf growth, with abnormal appearance associated with a slightly altered absorption of plant nutrients, both as to amount and ratio, the phosphate absorption being the more normal. The fertilizer combinations high in phosphate were the most effective in antagonizing the harmful effect of cumarin.

The dihydroxystearic acid also affected normal development, causing a decrease in top growth, but no abnormal appearance, the greatest abnormality being in this case observed in the root system, which was darkened and much stunted and showed swollen root tips, often bending into fishhooks, associated with a much altered absorption of nutrient elements both as to amount and ratio, the phosphate and potassium absorption being greatly depressed, the nitrate removal or disappearance being about as under normal conditions, but relatively much greater. The fertilizer combinations high in nitrate were the most effective in overcoming the harmful effect of this soil constituent.

In view of this widely different behavior of these two toxic substances, entailing the interesting observation that they responded differently to the different fertilizer combinations, it was thought desirable to consider some results with other toxic substances. In the first place, it was interesting to see whether the result observed with dihydroxystearic acid, namely response to the nitrate, was shown by another toxic body, and thus throw a little more light on this phase of the question. For this comparison the aldehyde vanillin was selected. This was known to be toxic from former experiments, was known to be oxidized by the plant roots, and was further known to be more readily oxidized when nitrates

were present,[5] and so should be a body which would behave much like dihydroxystearic acid.

In the present experiment with vanillin here recorded, the same number of cultures (66), containing all the fertilizer combinations possible in 10 per cent stages, was used as in the experiment with the dihydroxystearic acid and cumarin. The concentration of vanillin used was 50 ppm. The duration of the experiment was from March 7 to March 19. The solutions were changed every three days as in the cumarin experiment already described, but no analyses of the solutions were made in this case. The green weight, however, was recorded.

The effect of the vanillin was not so marked on the tops as on the roots, although in the regions of better growth this also was not very prominent. The general appearance of the plants resembles the effect produced by dihydroxystearic acid much more than the effect produced by cumarin under the same circumstances. The region of greatest growth appeared also, as in the case of dihydroxystearic acid, to be shifted toward the nitrogen end of the triangle. The plant growth was 84 per cent of the normal as an average of all the cultures.

For the present purpose, however, the growth in the cultures respectively high in phosphate, nitrate, or potash is of paramount interest. This grouping of the results obtained on the green weights at the termination of the experiment is shown in fig. 3. The relative growth in the cultures having 50 per cent and more of phosphate was 85 per cent of the growth without the vanillin; for the cultures mainly nitrogenous it was 88; and for the cultures mainly potassic it was 82. It will be observed that the vanillin depressed the growth least in the cultures high in nitrate, a result in harmony with previous observations on the toxicity of vanillin and in harmony with the action of dihydroxystearic acid. Both of these substances have reducing properties; that is, they are themselves readily oxidized; both have an inhibiting effect on root oxidation and on root growth generally; both are overcome by the fertilizer combinations which increase root oxidation to the greatest extent. It was consequently thought to be of interest to

[5] SCHREINER and REED, Jour. Amer. Chem. Soc. **30**:85. 1908.

see what the effect of an organic compound having oxidizing properties would be on plants growing in these various fertilizer combinations. For this purpose quinone, shown to be toxic to wheat seedlings in a former research, was chosen, inasmuch as it is an oxidizing substance and therefore in strong contrast to the vanillin with its decided reducing properties. This fundamental difference

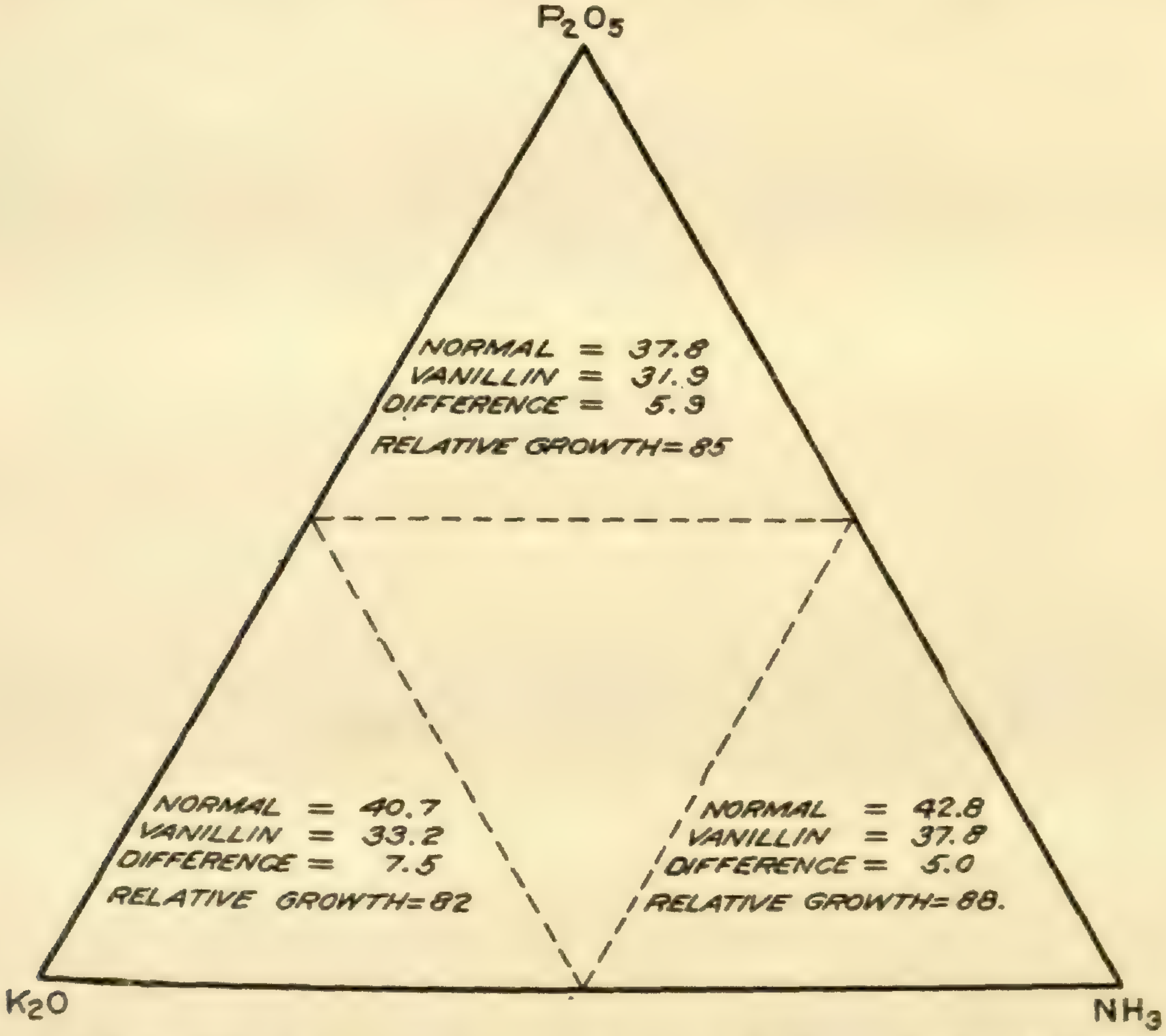

FIG. 3.—Showing the relative growth of normal and vanillin cultures in solutions high in phosphate, nitrate, or potash, respectively.

in the properties of the two compounds, it was thought, should show itself in an altered metabolism of the plants under the influence of two such widely different poisons, and the scope of the present experiment as to different fertilizer combinations should lend itself to showing such differences in metabolism or fertilizer requirement, and thus throw some light upon the behavior of crops in the field toward fertilizers under oxidizing conditions.

In the experiments with quinone the fertilizer combinations and

general technique were the same as in the preceding experiments with vanillin and cumarin, the concentration of quinone being 10 ppm. No analyses of the solutions were made in this experiment. The duration of the experiment was from March 23 to April 4.

The effect of the quinone on the development of the wheat was in itself as definite, though perhaps not as characteristic, as the effect of cumarin. The effect of the latter substance was to produce short, broad, irregularly developed leaves and stunted tops; the effect of the quinone was to produce long, thin leaves, producing tall, slender plants, so that at first glance the quinone in the concentration here used appeared to have had little effect on the growth of the plants. Closer inspection, however, shows the plants to be slender and weaker, although the leaves may be fully as long as the normal leaves. The effect of quinone on plant growth, however, is definitely shown by the decreased green weight. The root growth is also affected.

The most interesting feature of difference between the normal and quinone sets of cultures, observable when both sets are arranged in triangular form according to the composition of the culture solution, is the apparent or real shifting of the greater growth toward the potassium end of the triangle in the quinone set, accompanied by a generally better relative growth in the potash angle. This observation would seem to show that the quinone effect was counterbalanced by the fertilizer combinations high in potash, whereas cumarin was undoubtedly affected by the phosphate fertilizers, as shown, and vanillin as well as dihydroxystearic acid by the mainly nitrogenous fertilizers. This effect was not anticipated, but might easily have been, inasmuch as quinone is a strong oxidizing substance and potash salts are known from a previous research[6] to be retarders of root oxidation, analogous to the opposite effect of vanillin, a reducing substance overcome by nitrate known to stimulate root oxidation.

The green weights obtained at the end of the experiment bear out this observation. The relative growth in the quinone set was 75 per cent of the normal. The chief interest, however, centers

[6] SCHREINER, O., and REED, H. S., The rôle of oxidation in soil fertility. Bull. 56, Bureau of Soils, U.S. Dept. Agr. 1909.

in the comparative results obtained in the cultures containing 50 per cent and more of the phosphate, nitrate, and potash, respectively, in order to see which of these was the most efficient in antagonizing the action of quinone. The results of the grouping of cultures on this basis, made as explained in the preceding experiment, is shown in fig. 4. The mainly phosphatic fertilizer combinations show a relative green weight of 77 per cent of the normal,

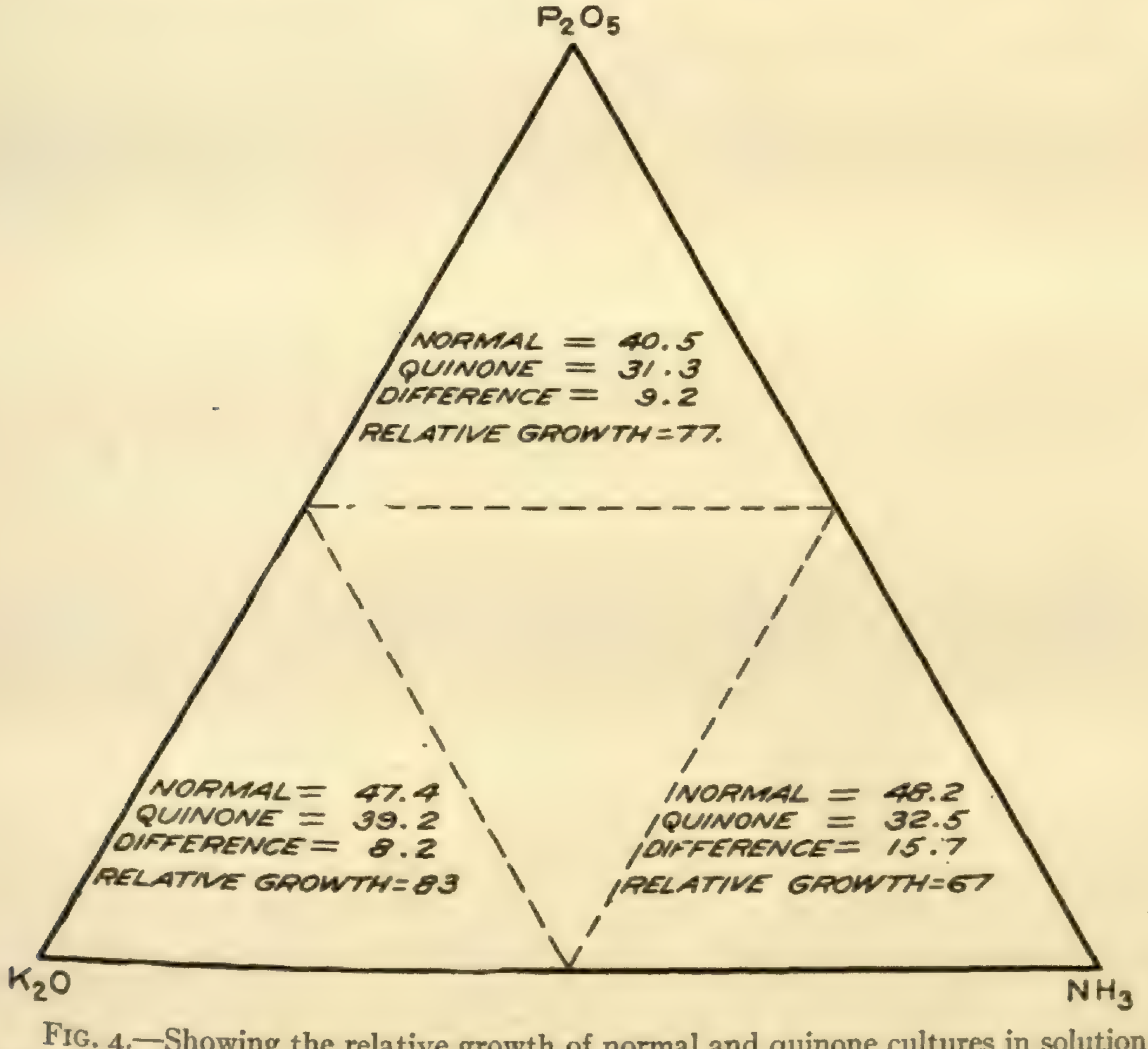

FIG. 4.—Showing the relative growth of normal and quinone cultures in solutions high in phosphate, nitrate, or potash, respectively.

the mainly nitrogenous 67, and the mainly potassic 83. It is observed that the potash fertilizers were the most efficient in overcoming the harmful effect of quinone.

This experiment with quinone was repeated, and this time the solutions were analyzed as in the case of the cumarin experiment. This second quinone experiment lasted from April 8 to April 20. It showed the same general slender appearance of the plants, as

well as again showing the influence of the potassium fertilizers as above described. In this experiment the green weight in the quinone set as a whole was 79 per cent of that in the normal. The results for the mainly phosphatic, mainly nitrogenous, and mainly potassic fertilizers are 76, 77, and 85, respectively, again showing the relative greater efficiency of the potash fertilizers in this quinone experiment.

These quinone experiments indicate clearly the harmful influence of quinone on growth, and the effect of potassium in counteracting this action of the quinone. In the second experiment the cultures were analyzed for phosphate, nitrate, and potassium, and it is, therefore, interesting to inspect these data, as was done with the cumarin results. Only the 36 cultures having the combinations of all three fertilizer salts are considered.

The amount of total $P_2O_5+NH_3+K_2O$ removed from solution by the growing plants in the total number of 36 cultures was 1568 milligrams in the normal set and 1327 milligrams in the quinone set, showing a decrease in the sum total of P_2O_5, NH_3, and K_2O removed when quinone is present. In table III are given the results for the P_2O_5, NH_3, and K_2O separately under the normal conditions and in the quinone set.

TABLE III

TOTAL MILLIGRAMS OF P_2O_5, NH_3, AND K_2O REMOVED FROM THE 36 CULTURE SOLUTIONS CONTAINING ALL THREE OF THESE INGREDIENTS

	TOTAL ABSORPTION IN MILLIGRAMS		RELATIVE	PERCENTAGE OF QUINONE CULTURES ABOVE NORMAL
	Normal	Quinone		
P_2O_5	300.4	173.6	58	8
NH_3	571.5	506.8	89	11
K_2O	696.5	646.5	93	36

An inspection of these figures indicates strongly that the potassium absorption in the presence of quinone has been more normal than the other two nutrient elements. This is shown both by the relative absorption in the third column and by the number of quinone cultures showing normal or greater absorption of P_2O_5, NH_3, and K_2O, respectively, in the last column.

We have, therefore, the interesting case of a toxic oxidizing body being overcome by a fertilizer salt having a restraining action on the normal oxidative power of the root, accompanied by a relatively greater absorption of this fertilizer element than under normal conditions.

Discussion and summary

In the foregoing experiments with cumarin, vanillin, and quinone, the effects of these toxic substances on the development of wheat seedlings was demonstrable by three criteria:

1. By decreased green weight.

2. By the morphological effects as shown by their general appearance. Cumarin-affected plants have characteristic stunted tops, broad, distorted leaves; vanillin-affected plants are less characteristic, but show decreased growth of top and strongly inhibited root growth; quinone-affected plants are tall and slender, with thin, narrow leaves, in strong contrast to the cumarin-affected plants. The substances show, therefore, a markedly different behavior in detail, although all show a toxic effect in inhibiting growth.

3. By decreased absorption of plant nutrients. The cumarin depressed potash and nitrate removal from nutrient solution more than phosphate; the quinone, on the other hand, depressed phosphate and nitrate more than potash; the effect of vanillin was not determined in this regard. It might be interesting to mention, however, that dihydroxystearic acid, which appears to act much as vanillin did, depressed phosphate, and potash more than nitrate. In this respect again the influence of the various harmful substances was different.

The various fertilizer salts acted differently in overcoming the respective harmful effects of these toxic compounds. The mainly phosphatic fertilizers were the most efficient in overcoming the cumarin effects; the mainly nitrogenous fertilizers in overcoming the vanillin effects; the mainly potassic in overcoming the quinone effects.

This different action of fertilizer salts on the toxic compounds is also illustrated by the diagrammatic representations in fig. 5 of the regions of greatest growth obtained in the various

experiments. The triangle represents the various cultures containing the fertilizer combinations, as is fully explained in fig. 1 and the accompanying text.

Under normal conditions, that is, without any toxic body present, the greatest growth is found in those cultures low in phosphate and about halfway between the nitrate and potash angles. This

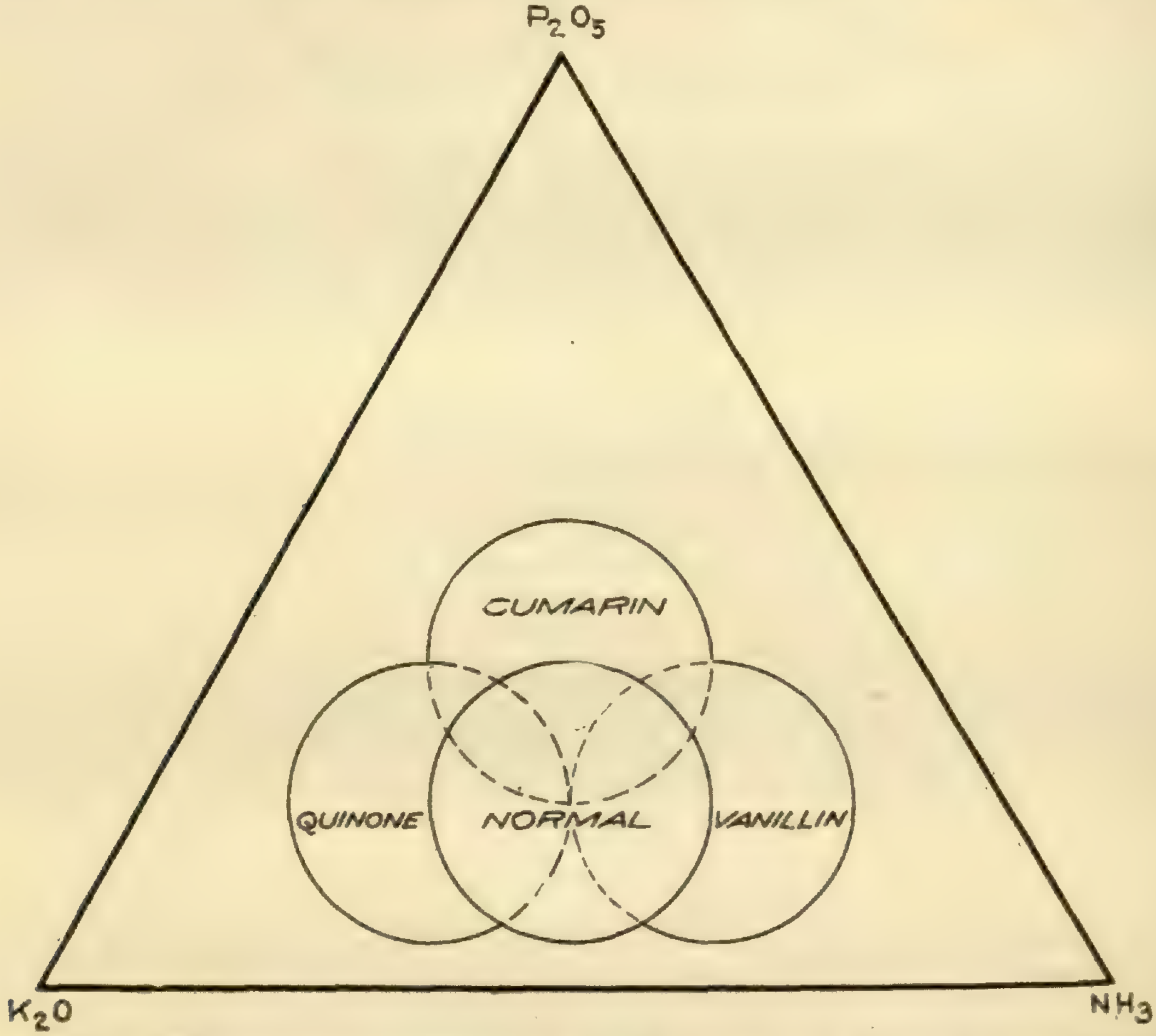

FIG. 5.—Diagrammatic representation of the region of greatest growth in the triangle culture experiments with cumarin, vanillin, and quinone.

region of greatest growth is diagrammatically represented by the circle marked normal in fig. 5. When cumarin is present in the cultures, the effect was to cause the region of greatest growth to shift in the direction of the phosphate angle, a condition which may be diagrammatically shown by the circle marked cumarin. With quinone, this region of growth was shifted toward the potash angle, and with vanillin toward the nitrate angle, as illustrated in the diagram.

This shifting of the region of greatest growth was accompanied by a corresponding change in the absorption of plant nutrients, although this is not as marked as the green weight. All of these facts are in harmony with the conclusion drawn from the data already given, that phosphate fertilizers were antagonistic to cumarin, that potash fertilizers were antagonistic to quinone, and that nitrate fertilizers were antagonistic to vanillin and to dihydroxystearic acid.

In regard to the exact mechanism of the chemical or physiological character of the interactions between these toxic substances and the fertilizer salts, nothing definite can be said. Attention, however, should be called in this connection to the fact that the reducing poisons vanillin and dihydroxystearic acid are antagonized by those fertilizer combinations which stimulate oxidation, and that the oxidizing poison quinone is antagonized by the fertilizer combinations checking oxidation, thus indicating that there is some correlation between these functions. A discussion of the interaction of cumarin and phosphate fertilizers would be mere speculation in the present state of our knowledge.

Attention must also be called again to the fact that the observations here recorded for phosphate, nitrate, and potash were obtained with the salts, calcium acid phosphate, sodium nitrate, and potassium sulphate, and that the observed results, therefore, may be caused by these substances as a whole, that is, as combinations rather than individual elements. For deciding this question, further investigation is necessary, involving experiments with other salts and combinations.

These actions of the different fertilizer combinations or different fertilizer requirements, as they may be styled, show a certain parallelism with field observations on soils and their fertilizer requirements, and one is tempted to ask to what extent may the different fertilizer requirements of different soils or of the same soil under different conditions be influenced by the same cause. That harmful bodies occur in soils has been amply shown, and that these are influenced directly or indirectly by fertilizer salts is also clear from this and other researches. That the constitution of the organic matter varies from soil to soil, and in the same soil under

different conditions of aeration, drainage, and cropping, is likewise clear. The presence of compounds inimical to plant growth by virtue of a property resembling that of any of the above-mentioned poisons might therefore cause a different fertilizer requirement, a requirement which might even change from time to time according to the nature of the biochemical reactions producing the body, or according to the nature of the plant remains in the soil; in other words, according to rotation, with its necessary altered soil management, and the altered biochemical changes produced in the different plant remains.

The action of fertilizers on soils is a much contested question, but the weight of evidence is against the assumption that their effect is due altogether to the added plant food. If so simple an explanation were the true one, nearly a century of investigation of this problem by scientists of all civilized nations would surely have produced greater unanimity of opinion than now exists in regard to fertilization. Thoughtful investigators everywhere are finding that fertilizer salts are influencing many factors which contribute toward plant production besides the direct nutrient factor for the plant. It is this additional influence of fertilizers which makes them doubly effective when rightly used and inefficient when improperly used. To this influence of fertilizers on soil and biological conditions is due their capriciousness when applied on the theory of lacking plant food, and any study which throws further light upon the mooted question is of direct help toward reaching that view of soil fertility and soil fertilization which will eventually result in a more definite system of fertilizer practice, to the end that surer and safer returns are obtained from their use. This will tend to extend fertilizer practice by making it more remunerative and rational than in the past.

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THE EFFECT OF EXTERNAL CONDITIONS UPON THE AFTER-RIPENING OF THE SEEDS OF CRATAEGUS MOLLIS

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WILMER E. DAVIS AND R. CATLIN ROSE

It is well known that the seeds of many plants do not germinate immediately after ripening, but only after a period of rest which in some cases no doubt extends into years. NOBBE and HANLEIN (**16**), for example, kept certain weed seeds under germinating conditions for a period of 1173 days without germination.

While various workers have done much in the way of adding to the list of seeds that require a rest period before germination, little has been done to determine the real cause of this delay or dormancy on the part of the seed. During this period, it is assumed that the seed undergoes certain changes, at the completion of which germination may take place. This period of preparation for germination has been termed the after-ripening period. The term after-ripening then may be made to include the necessary protoplasmic changes antecedent to germination; changes involving the release of digestive and respiratory enzymes, thus leading to rapid metabolism; or disintegration or other modifications of incasing structures that limit the water or oxygen supply or even mechanically hinder growth. But in relatively few cases do we know to which of these dormancy is due. In most literature the cause is assumed to be the need of protoplasmic changes in the embryo. In this paper we have used the term after-ripening in reference to embryonic changes whether protoplasmic or metabolic, in contrast to those changes that merely affect the incasing structures. By germination we mean the growth of the hypocotyl.

Many more or less successful attempts have been made to shorten or eliminate altogether this period of inactivity on the part of the embryo by certain stimuli designed to arouse the dormant protoplasm to activity. Lately FISCHER (**5**) observed that seeds of certain water plants might be kept in water free from fermentation

for years without germination, but if fermentation were set up, the seeds would soon after begin to germinate. He attributed this to the effect of H+ or OH− ions acting as stimuli on the dormant protoplasm. MÜLLER (15) found that the seeds of *Eichhornia* and *Heteranthera* germinate only after desiccation. CROCKER (1), working on the seeds of various water plants, including *Eichhornia* and others reported by FISCHER, has shown that the protoplasm is not dormant. He found that the seeds of *Eichhornia*, *Alisma Plantago*, and *Sagittaria* germinate readily in distilled water if the coats were broken, and concluded that bases and acids here must have their effect upon the seed coats rather than upon the embryos. He also concluded that the effect of the coats in many of the seeds of water plants is mainly to limit the water rather than oxygen supply, since little if any oxygen is needed by them for germination.

KINZEL (11) and HEINRICHER (8) have shown that in many seeds light is necessary for germination. Seeds kept under ordinary germinating conditions for months in darkness failed to germinate, but when placed in light germinate within a few days. Both KINZEL and HEINRICHER seem to have taken it for granted that the changes induced by the light have to do with the embryo. But even here it is barely possible that light in some way affected the seed coat, rendering it permeable.

It has long been known that cold has an influence in some way on the germination of various seeds. Many seeds are thought to germinate only after being subjected to freezing and thawing. But as to the exact effect of the cold in bringing about germination there is as yet nothing very definite.

PAMMEL and LUMMIS (17) found that many weed seeds that failed to germinate under ordinary germinating conditions germinated more or less readily after freezing. PAMMEL and KING (18) have shown that freezing and thawing not only increase the percentage of germination in many weed seeds, but that the seeds thus treated in many cases germinate more quickly than those kept dry before planting. FAWCETT (4) likewise has shown that freezing and thawing shortens the dormant period of many weed seeds, and that the percentage of germination of seeds exposed to

the weather is in many cases considerably higher than of those kept dry. In wild rye, for instance, the dormant period was reduced from 9 to 5 days, and the percentage of germination was raised from 2 to 48. But the limiting factors to growth have not been located in any of these cases.

Investigation

This work on the germination of the seeds of the hawthorn (*Crataegus mollis*) was undertaken in order to determine so far as possible the influence of the various external conditions affecting their after-ripening. Hawthorn seeds usually do not germinate until the second or even third year after the fruit has ripened. KUNTZE (**14**) wrote in 1881: "Hawthorn berries (*Crataegus*) which do not germinate until the second year are peculiarly treated. They are mixed with sand, thrown into a heap, and watered a few times in a cold house during the winter, and sown the following spring. They are turned over several times so that the pulp may decompose." The *Cyclopedia of American horticulture* (**3**) also refers to this delay in the germination of the seeds of the hawthorn and gives the method employed in their germination essentially as that given by KUNTZE.

In considering the after-ripening and germination of the hawthorn, the various structures about the seed, as the pericarp and carpels, as well as the testa and embryo itself, must not be overlooked. The pericarp is separated from the carpels by decay or by being eaten off by some animal. It often shrivels and remains intact for a considerable length of time. The carpels are bony and the seed is freed only after much weathering, when the carpels become more or less porous to water and are split by the swelling of the seeds. Both of these structures in nature, by the prevention of a sufficient supply of water and oxygen, may tend to prolong after-ripening as well as delay germination.

Our first work was to determine the behavior of the seeds under ordinary germinating conditions. To do this we removed the pulp and the bony carpel. The seeds were than placed upon wet cotton in Petri dishes, both in the laboratory and the greenhouse. They remained in this condition for months without any sign of germina-

tion, and all those seeds that had suffered injury, however slight, in removing them from the carpels invariably decayed.

To remove the possibility of coat effects, we next removed the testas and treated the embryos as above; when thus treated an occasional hypocotyl grew, varying from none to 3 or 4 per cent. CROCKER (**2**), who previously employed this method, indicated a higher percentage of growth. The behavior of the embryos under these conditions as pointed out by him is interesting in that it shows a remarkable correlation between the cotyledons and the hypocotyl. In the light the cotyledons soon turn a dark green and enlarge often to several times their original size. The hypocotyl does not elongate, but remains short and blunt. In case of germination after complete after-ripening, the hypocotyl takes precedence and elongates rapidly, while the cotyledons increase in size much more slowly and never reach the size attained in case the hypocotyl fails to elongate. In darkness the behavior was similar, except that the cotyledons contained xanthophyll.

We next carried on experiments to determine the effect of low temperatures in bringing about after-ripening and germination. The first set of experiments was carried on in an ordinary ice chest so arranged as to admit light to some of the cultures. With this we were able to obtain a temperature of 5°–6° C.

In all cases the seeds treated were placed on wet cotton in Petri dishes or in air-tight jars, excepting those seeds that were subjected to low temperatures in a dry state or under water. These were treated in test tubes with cotton plugs. Table I gives the results of the first set of experiments.

In these cultures the number of seeds germinated compared with the total number treated may seem rather low, varying as they do from 50 to 80 per cent. This is not due to the seeds failing to germinate when removed from the cold, but almost entirely to loss during the process of after-ripening. It is quite difficult to remove the seeds from the carpels without injuring them. While in all cases they were removed by carefully splitting the carpels with the point of a strong knife, yet many suffered more or less injury that escaped observation until placed upon the ice. The seeds with their testas broken invariably decayed during the pro-

cess. Seeds with the testas broken decay more readily than those with the testas removed, because the edges of the broken testas offer a good lodging-place for bacteria and the spores of various fungi. The seeds during the after-ripening process require considerable care. They should be removed occasionally, washed, sorted, and placed upon clean wet cotton. They are especially liable to decay if they are left in a mass. The loss in after-ripening can be greatly reduced by thoroughly washing the seeds before placing them in the cold.

TABLE I

No. culture	No. seeds	Condition of seeds under treatment	Temperature	No. days at low temperature	In light	In dark	Germination within 10 days	Total number germinated after 20 days
14....	400	Carpels off.....	5–6°	96	—		221	264
13....	400	Carpels on.....	5–6°	242	—		0	0
18....	400	Carpels off.....	5–6°	96		—	122	250
17....	400	Carpels on.....	5–6°	242		—	0	0
9....	400	Carpels off.....	5–6°	96		—	5	219
8....	400	Carpels off.....	5–6°	96		—	244	311
16....	400	Carpels off (seeds dry)..	5–6°	96		—	0	0
19....	400	Carpels off (seeds under water).....	5–6°	150		—	0	0

Germination at 10°–12° C.

When the seeds had been left a sufficient time in the cold to after-ripen, the percentage of germination based upon the number coming from the cold was always high, running from 90 to 98 per cent.

When the above seeds were removed from the cold and were placed in a water bath at a temperature of 10° to 12° C. to germinate, practically all the seeds, except those treated dry or under water or with carpels on, germinated, but the time required was somewhat extended. In later experiments, where seeds were removed from the cold to the temperature of the greenhouse, the period of germination covered a much shorter time, as will be seen in table II.

The seeds treated under water and those treated dry showed no signs of after-ripening; when they were removed from the cold, they decayed. The failure to after-ripen under water was probably due to an insufficient supply of oxygen. Seeds treated with carpels

on showed considerable progress in after-ripening. During the latter part of the period in the cold there was occasional germination, and when the carpels and coats were removed, the embryos generally responded normally.

TABLE II

No. culture	No. seeds	Temperature	No. days at low temperature	Germination within 5 days	Germination within 10 days	Remarks
1.....	150	5–6	73	109	112	
2.....	150	0	73	45	68	
21.....	150	0	90	82	83	
4.....	150	−2 to −3	75	0	0	
23.....	150	−2 to −3	77	0	0	
24.....	150	−2 to −3	114	0	0	
10.....	150	5–6	130	0	0	Treated without oxygen
20.....	150	5–6	130	0	0	Treated H_2 with 2 per cent oxygen
5.....	150	5–6	90	5	5	Treated without oxygen
3.....	150	0	90	0	0	Treated without oxygen
7.....	150	0	90	0	0	Treated H_2 with 2 per cent oxygen

The above experiments were conducted in an ice chest so constructed that by means of salt three fairly constant temperatures were obtained: 5° to 6°, 0°, and −2° to −3° C. The seeds were freed from the carpels and after-ripened in the dark.

It will be noticed that the time the seeds were left in the cold to after-ripen is in some cases less than that in the previous table, and also that the seeds germinated more quickly when removed from the cold. The seeds were removed from the cold directly to the greenhouse instead of the bath, as in the first set of experiments.

In culture no. 1, 109 seeds responded within 3 days, and the 3 remaining within 5 days. Not more than 2 or 3 seeds decayed after they were removed from the cold. The average length of the hypocotyls after 5 days was 15 mm. In no. 2, the germination was slower, the hypocotyls elongated less rapidly, and many decayed when taken from the cold. No. 21 remained 17 days longer in the cold than no. 2, which no doubt accounts for the greater number germinated. Nos. 4, 23, and 24, although left at the low temperature from 75 to 114 days, showed no signs of germination.

Nos. 10, 20, 5, 3, and 7 were arranged to determine the relation of oxygen to after-ripening. The seeds in these cultures were placed on wet cotton in Novy jars of about a liter capacity. Nos. 10, 5, and 3 were without oxygen. The oxygen in no. 5 was removed by pyrogallate. In nos. 10 and 3 the jars contained hydrogen washed in pyrogallate. No. 20 contained hydrogen washed in KOH and $KMnO_4$. The hydrogen used was from the Linde Air Products Company of Buffalo, N.Y. Upon analysis it was found to contain 2 per cent oxygen. The results with no oxygen or even 2 per cent were mainly negative.

Several cultures were treated with ether in addition to the cold. The seeds were placed in air-tight jars of a liter capacity. In each jar there was a small bottle containing 10 cc. of water, to which had been added ether varying in the different cultures from 0.25 cc. to 1 cc. The jars were then placed in the cold from 8 to 16 days. At the end of this period the seeds were removed from the jars, placed in Petri dishes, and returned to the cold. The germination in every case was less than that of the control culture without ether. While ether may have a stimulating effect upon germinating seeds, the concentrations used here retarded rather than hastened after-ripening.

To determine the effect of a temperature upon after-ripening somewhat higher than the ones previously employed, the following cultures were placed in a water bath December 1 in which the temperature at the beginning was 9°–10° C. Tap water was used in the bath and the temperature varied with the season, ranging from the above temperature to as high as 22° C. in July and August. The seeds were freed from the carpels. Table III shows the results of these experiments. As fast as the seeds were after-ripened and germinated, they were counted and removed from the bath.

All these cultures were put in the water bath December 1, excepting no. −1, which was placed there 10 days later. This gave it 10 days less exposure to the low temperature at the beginning, and this in part, at least, may account for the difference in the number of seeds germinated between it and no. 1. There is also brought out in this table a very marked falling off in germination as the temperature rose, which means, of course, a similar falling

off in the number of seeds after-ripened. Several of the seeds that germinated late in the season had rather stunted hypocotyls. The difference in the number of seeds germinated in the light and the dark at these temperatures seems to indicate that light at least at these temperatures had some influence on the after-ripening.

TABLE III

No.	No. seeds	Carpels		Temp.	No. days in bath	Light	Dark	Germination during						Total
		On	Off					Mar.	Apr.	May	June	July	Aug.	
1..	400		/	9–22° C.	275	/		40	25	15	11	11	1	103
—1..	400		/	9–22° C.	264	/		8	9	12	17	11	3	60
2..	400		/	9–22° C.	275		/	9	1	0	7	1	1	19
3..	400	/		9–22° C.	275	/		5	2	0	0	0	0	7
4..	400	/		9–22° C.	275		/	0	0	0	0	0	0	0

To determine the effect of alternating high and low temperatures, a culture (no. 9) was placed in the above water bath April 13. The temperature of the bath at this time was about 13° C. It was left at this temperature for 10 days, when it was removed to the ice chest at a temperature of about 6° C. This 10-day alternation was kept up until September, or for 140 days. None of the seeds germinated during this time, although they had been exposed one-half of that time, or 70 days, to a temperature most suitable for after-ripening. The high temperatures appear to have counteracted the effect of the low temperatures.

In order to ascertain the importance of the testas in after-ripening, they were removed from 50 seeds and the embryos were placed in the cold at a temperature of about 6° C. At the end of 28 days several of the embryos showed signs of germination. They were then removed from the cold to the greenhouse, and within 10 days 39 of the 50, or 78 per cent of the seeds treated, had germinated. The time required for after-ripening seeds without testas was about one-third of that required for seeds with testas, under conditions otherwise the same.

In the after-ripening of these embryos the correlation between cotyledons and hypocotyl was made very evident. The embryos to after-ripen must be kept at a temperature sufficiently low to inhibit growth in the cotyledons. When the embryos were exposed

but a short time to high temperature, the cotyledons began to enlarge, and if exposed to light to turn green and after-ripening would not take place.

The importance of water as a factor in the after-ripening of the seeds of the hawthorn needs to be emphasized. Those seeds kept thoroughly wet during this process gave the best results, as indicated by the germination when removed from the cold. The prolonged period of after-ripening of seeds within the carpels, the shorter period when the carpels were removed, and the still shorter period when both carpels and testas were removed show that these structures add greatly to the resting period. In order to determine to what extent the carpels and testas interfered with the taking up of water by the embryo, we took two lots of seeds, one with the carpel intact, and the other with carpels removed. Each lot was soaked in water at room temperature for 48 hours. The testas were then removed from a portion of the second lot. These three sets of seeds, one with carpels intact, one with testas, and the other with both carpels and testas removed, were placed upon wet cotton in Petri dishes and left in an ice chest at about 7° C. for 14 days. At the end of this period the carpels and testas were removed from all seeds which had been treated with them on, and the water content of the embryos determined for the three conditions. The embryos were dried in vacuo over H_2SO_4. The determinations were made in duplicate and are given in table IV.

TABLE IV

No. seeds treated	Condition of embryos during treatment	Wet weight of embryos in grams	Dry weight of embryos in grams	Water content in grams	Water content in percentage
42	Carpels on	0.5114	0.3844	0.127	24.8
25	Carpels on	0.3186	0.2396	0.0796	24.9
29	Testas on	0.4018	0.2730	0.1278	32.5
44	Testas on	0.6056	0.4180	0.1876	30.9
44	Testas off	0.6866	0.4100	0.2766	39.4
30	Testas off	0.4810	0.2904	0.1906	39.6

GASSNER (**6**) has shown that seeds of two South American grasses, *Chloris ciliata* and *C. distichophylla*, after-ripen in dry storage. The most favorable period of dry storage was found to be 30–40 weeks. He also found light to be an important factor

in their germination when removed from dry storage, light favoring and darkness hindering germination. After 10 weeks of dry storage, there was no germination in darkness at the optimum temperature, but after 39 weeks, 7–8 per cent germinated under the same conditions. In light after 9 weeks of dry storage, 73 per cent germinated under the same conditions. In a recent article (**7**) covering a study of *Stenotaphrum glabrum* and *Paspalum dilatatum*, GASSNER found that *P. dilatatum* after-ripened in 1 to 2 weeks in dry storage at 50°–60° C.

The after-ripening of these seeds in dry storage is most interesting, especially if it is a true case of after-ripening, that is if the cause of delay lies in the embryo rather than in the coat. If the delay were due to an impermeable coat, it would not be difficult to understand how drying might cause it to rupture or change otherwise its permeability to water or oxygen. The presence of water is usually necessary to initiate chemical changes. This is especially true for germination, and in the hawthorn, at least, is also true for after-ripening, since neither the seeds kept dry for long periods at the temperature of the laboratory nor at temperatures most favorable for after-ripening showed any signs of germination when placed under germinating conditions.

The claim that certain seeds after-ripen in dry storage is quite general. KINZEL (**13**) found that for oats kept in dry storage the percentage of germination increased for 8 months after harvesting and then gradually fell. But in all these cases there is need of a thorough analytical study of the processes involved in the after-ripening.

Some general considerations

The preceding tables indicate that the after-ripening in the hawthorn takes place at low temperatures, the optimum for which is 5° to 6° C. But the process goes on even at 0° C., while at −2° C. to −3° C. it makes little or no progress. Freezing and thawing, then, do not appear to be the ideal conditions for after-ripening. The value of freezing and thawing to seeds which are lying in the soil, in which cold is a factor in the after-ripening, very likely consists in rupturing the seed coat or other external structures, by means of which water or oxygen are permitted to enter. Especially

is this true of seeds in which the cause of the delay is in the external structures rather than in the embryo. In the hawthorn, freezing and thawing undoubtedly bring about a splitting of the bony carpels sooner than would otherwise occur, and in this manner shorten the period of after-ripening.

Temperatures alternating between that most favorable for after-ripening, as 5° to 6° C., and temperatures ranging from 13° to 22° C. were not favorable to after-ripening. While we did not employ other alternating temperatures than those above, we are led to believe that there is always some favorable constant temperature at which after-ripening will take place most readily, and that any variation from this temperature either above or below will retard it.

There is considerable variation in the time in which individual seeds after-ripen, as is indicated in table III and again in those seeds that were removed from the cold too soon. In the latter case there was always a large number of seeds that failed to germinate. These in nearly all cases would germinate if the testas were removed, but when not so treated and left at high temperatures, they would lie upon the moist cotton for weeks without germinating. The higher temperatures seem to inhibit the process of after-ripening. The process of after-ripening then is interesting in that it does not obey the VAN'T HOFF temperature law for rate of chemical reactions, but goes on faster at low temperatures. If this temperature law applies to the individual metabolic processes involved in after-ripening, it must apply to them with quite different coefficients, with the general result that the process as a whole falls with a rise of temperature.

While the results with low oxygen pressure were mainly negative or nearly so in all cases, we are not prepared to say that after-ripening cannot take place under low oxygen pressure or even in the entire absence of oxygen if sufficient time is allowed, but oxygen certainly favors after-ripening. We are now carrying on experiments to determine more definitely the various points in reference to after-ripening and oxygen pressure.

Light does not seem to enter into the after-ripening of the hawthorn to any great extent. At the optimum temperature after-

ripening goes on equally well in dark or light. At a temperature considerably above the optimum, but not sufficiently high to stop the process altogether, light does appear to have some influence, as is indicated in table III.

The seeds of the hawthorn will germinate at a temperature slightly above 0° C. We have found them in nature germinating in early spring, when the ground was yet quite cold and wet. Seeds placed on ice for after-ripening germinate in this condition after going through that process. The germination, however, takes place irregularly, and often requires a considerable period before all the seeds of the culture are germinated. But if the seeds are removed from the cold when they show signs of germinating, and placed at the temperature of the greenhouse, the germination takes place very rapidly, often reaching 90 per cent or more within two or three days. The sudden change of temperature when the after-ripening is complete acts as a powerful stimulus to germination, but if after-ripening is not complete, it seems to inhibit the latter.

How widespread this condition of seeds is, which requires after-ripening, that is, some change involving the embryo itself before germination becomes possible, is not known. All seeds that are slow to germinate, from whatever cause, have too frequently been put into this class. In most cases the delay is evidently not to be found in the embryo at all, but in the seed coat or some other external structure which prevents or limits the taking up of water or oxygen or mechanically inhibits growth. The only way to determine whether the delay is due to after-ripening or to hindrance of incasing structures is to remove the external parts and subject the embryo to germinating conditions.

Dr. ECKERSON of this laboratory is making a study of the internal changes that take place in the seeds of the hawthorn during the process of after-ripening. The work is now well under way.

Conclusions

The seeds of the hawthorn do not germinate immediately after the fruit has ripened, but have a latent period of one or more years.

The cause of the delay is very largely in the hypocotyl rather than in the cotyledons or any of the external structures.

If the seeds are removed from the carpels and kept very moist and at a temperature of 5° or 6° C., the latent period may be shortened to 2.5–3 months, and if the testas are removed and the embryos treated, the period may be reduced to 30 days. Temperatures below 0° C. are not favorable for after-ripening. Seeds kept at −2° to −3° C. did not after-ripen. Seeds at 0° C. after-ripened, but not so readily as those kept at a few degrees above 0° C. The most favorable temperature for after-ripening seems to be 5°–6° C.

Low temperatures alternating with high temperatures are not favorable for after-ripening.

If the seeds are removed from the cold chamber before they have passed through the after-ripening period and subjected to the temperature of the greenhouse, the high temperature either stops or greatly retards the process of after-ripening.

If the seeds are completely after-ripened and removed from the cold to the temperature of the greenhouse, they germinate very quickly. The high temperature greatly stimulates the process of germination.

After-ripening readily takes place under ordinary oxygen pressure, but it has not been fully determined to what extent the oxygen pressure may be reduced and the process still go on.

The pulp, carpels, and seed coat itself tend to delay the process of after-ripening, probably by preventing the free access of water. The changes that take place in the embryo during the after-ripening are not yet known.

Seeds treated dry as well as those treated under water did not after-ripen.

While after-ripening and germination in the hawthorn is a continuous process, that is, we cannot tell where one leaves off and the other begins, the optimum temperature for the latter is considerably above the optimum for the former.

In conclusion, we wish to express our thanks to Dr. WILLIAM CROCKER, at whose suggestion this work was undertaken and who offered many valuable suggestions during its progress.

THE UNIVERSITY OF CHICAGO

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THE STRUCTURE OF THE STOMATA OF CERTAIN CRETACEOUS CONIFERS[1]

W. P. THOMPSON

(WITH PLATES V AND VI)

The structure of the stoma is remarkably uniform in all members of the plant kingdom, from *Anthoceros* to the highest angiosperms. It consists essentially of an aperture surrounded by two guard cells which may be more or less sunken and protected by adjacent cells. The only deviation from this organization has been described for the fossil genus *Frenelopsis*, first by ZEILLER,[2] and more recently by BERRY.[3] These authors state that in place of the usual two guard cells, each stoma of *Frenelopsis* is surrounded by four or five guard cells in the form of a rosette. The uniqueness of this supposed condition made it desirable that the subject should be reinvestigated, and for this purpose I have had access to material of *Frenelopsis occidentalis* (Heer), supplied by Professor ZEILLER from a collection made at Nazareth, Portugal, by Professor CHOFFAT.

The characters of the genus *Frenelopsis* have been given in detail by ETTINGSHAUSEN,[4] SCHENK,[5] and others. It is a cretaceous conifer of disputed affinities, being referred by some authors to the Cupressineae and by others to the Gnetales. The leaves are decussately arranged in twos or fours at the nodes of the jointed stem. They are reduced, squamiform, and appressed. The internodes functioned as leaves.

The epidermal characters of *Frenelopsis occidentalis* have been

[1] Contributions from the Phanerogamic Laboratory of Harvard University, No. 45.

[2] ZEILLER, R., Observations sur quelques cuticules fossiles. Ann. Sci. Nat. Bot. **6**:13. 1882.

[3] BERRY, E. W., The epidermal characters of *Frenelopsis ramosissima*. BOT. GAZ. **50**:305–309. *figs 2*. 1910.

[4] ETTINGSHAUSEN, C., Abhand. k.k. geol. Reichsanstalt. Vol. I.

[5] SCHENK, H., Palaeontogr. **19**:13. —.

described by ZEILLER.[6] The cells are rather small, roughly rectangular, and very thick-walled. The very numerous stomata are arranged in irregular lines which give a striated appearance to the unmagnified specimen.

A single stoma is shown in surface view in fig. 1. The central aperture is surrounded by the five "guard" cells of BERRY and ZEILLER. A conical projection can be distinguished extending from each cell to the common center and together forming the rosette. These projections are really below the surface, and, since they are in focus, the opening at the surface is indistinctly seen above them as a pentagonal area whose walls coincide with the bases of the cones.

A clearer idea of the relation of the parts may be obtained from fig. 2, which is a photograph of a vertical section through one of the stomata. The conical processes of the so-called "guard" cells are here seen to project into the middle of a cavity. At the upper limit of this cavity, that is, at the surface, the epidermal cells again approach each other to form, not conical projections, but the pentagonal opening seen indistinctly in the photograph of the surface. These complicated cells are regarded by both BERRY and ZEILLER as guard cells, obviously unlike the guard cells found anywhere else in the plant kingdom. ZEILLER compares them with those of *Marchantia* as follows:

> Le seul fait qui me semble avoir quelque analogie avec cette constitution particulière des stomates, serait celui qu'on observe chez les Marchantiées, où les pores stomatiques sont bordés par cinq ou six cellules, mais qui laissent entre elles une ouverture en forme de canal, et non pas une fente en étoile, comme dans l'espèce dont je viens de parler. Il serait cependant assez singulier et assez peu vraisemblable que cette forme étoilée des stomates fût un fait isolé, n'existant que chez le seul *Frenelopsis Hoheneggeri*, et peut-être faut-il s'attendre à la retrouver quelque jour sur d'autres plantes fossiles, sinon même dans la nature vivante.

In his conception of their arrangement, BERRY disregards that part of the cell above the diverticulum, although he figures it in his low-power drawing.[7] Aside from their unique number and disposi-

[6] ZEILLER, R., Elements de palaeobotanique. Paris. 1900.

[7] *Loc. cit.*, p. 307.

tion, it is difficult to imagine how these structures could effectually serve as guard cells.

The proper conception of the arrangement and homologies of these parts may be most easily obtained from an examination of living forms. The conditions existing in *Agathis bornensis* are represented in fig. 6, which is a photograph of a vertical section of the base of the leaf of that species. The two conspicuous oval cells almost in contact are the sunken guard cells. Inclined above them, with their small extremities at the strongly cutinized surface, are the accessory cells. Each of the latter is seen to have a slight *projection* into the cavity some distance above the guard cells. Viewed from the surface (fig. 7), the accessory cells are seen to be *four* in number surrounding the opening. From the same viewpoint, the guard cells (fig. 8) are seen to be *two* in number, and arranged in the usual manner.

These conditions at once suggest that the so-called guard cells of *Frenelopsis* are really accessory cells, and that we must look below them for the true guard cells. As stated by both BERRY and ZEILLER, structural material of the epidermis only is available, so that the depressed guard cells are not likely to have been preserved. Nevertheless, diligent search reveals their presence in many favorable specimens. Fig. 3, which is a photograph of another stoma in section, shows two well-preserved guard cells at the bottom of the cavity into which the cònical structures project. Fig. 4 shows another stoma with unmistakable guard cells below the accessory cells. In this figure the end of a projection from another accessory cell has been cut off and appears in the center of the stomatic cavity. In the majority of the stomata examined in section, no guard cells can be distinguished; in others, fragments have been preserved, especially the outermost wall, which appears to have been more strongly lignified; in still others, the whole structure is preserved in exactly the relations which one would expect in living material.

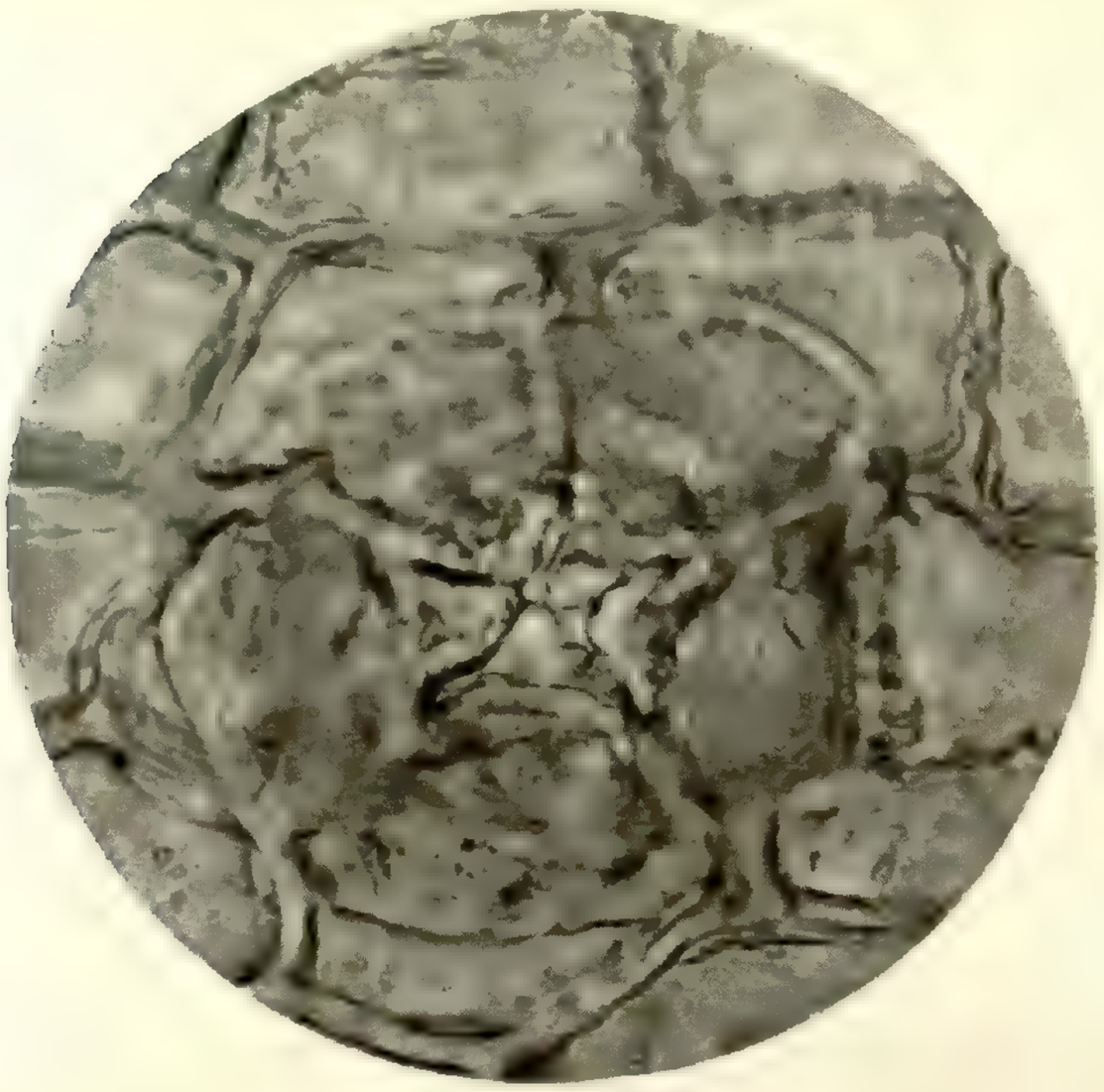
It is still more difficult to observe the guard cells in surface view, owing to the fact that they are covered by the extremely thick accessory cells. This circumstance also entirely precludes their reproduction by photograph. Nevertheless, examination of the

epidermis from beneath reveals their presence in a condition of good preservation in some instances, and of imperfect preservation in many others. A camera lucida drawing showing their typical arrangement above the accessory cells (below in nature) is presented in fig. 5. They are seen to have the normal form. The thinness of their walls probably accounts for the imperfect state of preservation.

That true guard cells of the normal form are present in *Frenelopsis*, in addition to the remarkable accessory cells, is further indicated by the similar conditions presented by other cretaceous plants. A case in point is furnished by *Androvettia statenensis* Hollick and Jeffrey. Fig. 9 is a photograph showing the general features of the epidermis of the species. The cells are very thick-walled and irregular in shape. The numerous stomata lack the definite arrangement characteristic of *Frenelopsis*. The more highly magnified representation given in fig. 10 shows the presence of accessory cells around the stomata as before. In this case they lack the conical projections of *Frenelopsis*, the opening having a uniform outline. The presence of true guard cells is strikingly illustrated in the figure, the aperture appearing as a conspicuous slit across the space surrounded by the accessory cells. Owing to the good condition of preservation of this plant, the guard cells are distinguishable in the majority of cases. Nevertheless, in poorly preserved specimens they have often been destroyed just as in *Frenelopsis*. Fig. 11 shows two stomata from which the guard cells have completely disappeared, although the accessory cells are present in their normal condition.

Another cretaceous fossil possessing both true guard cells and accessory cells is *Brachyphyllum macrocarpum* Newberry. A section parallel to the surface of the leaf of this plant is shown in fig. 12. In each of the stomata the two guard cells are seen to be surrounded by four accessory cells.

The evidence herein adduced from the structure of the stomata of modern conifers, from the conditions presented in fossils of the same geologic age, and above all from actual observations both in section and surface views of *Frenelopsis* itself, appears to show conclusively that true guard cells are present in this genus, and that the



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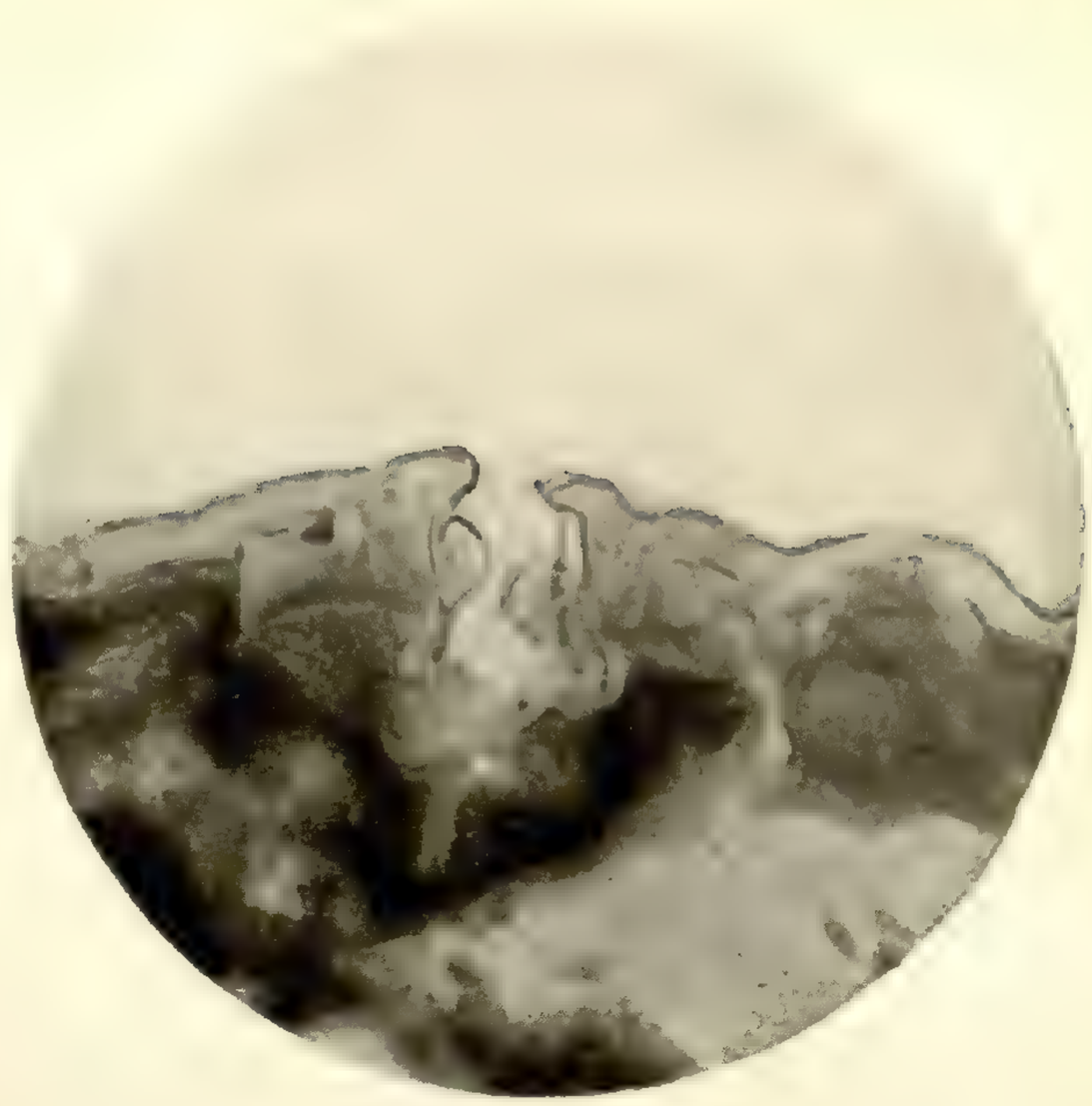

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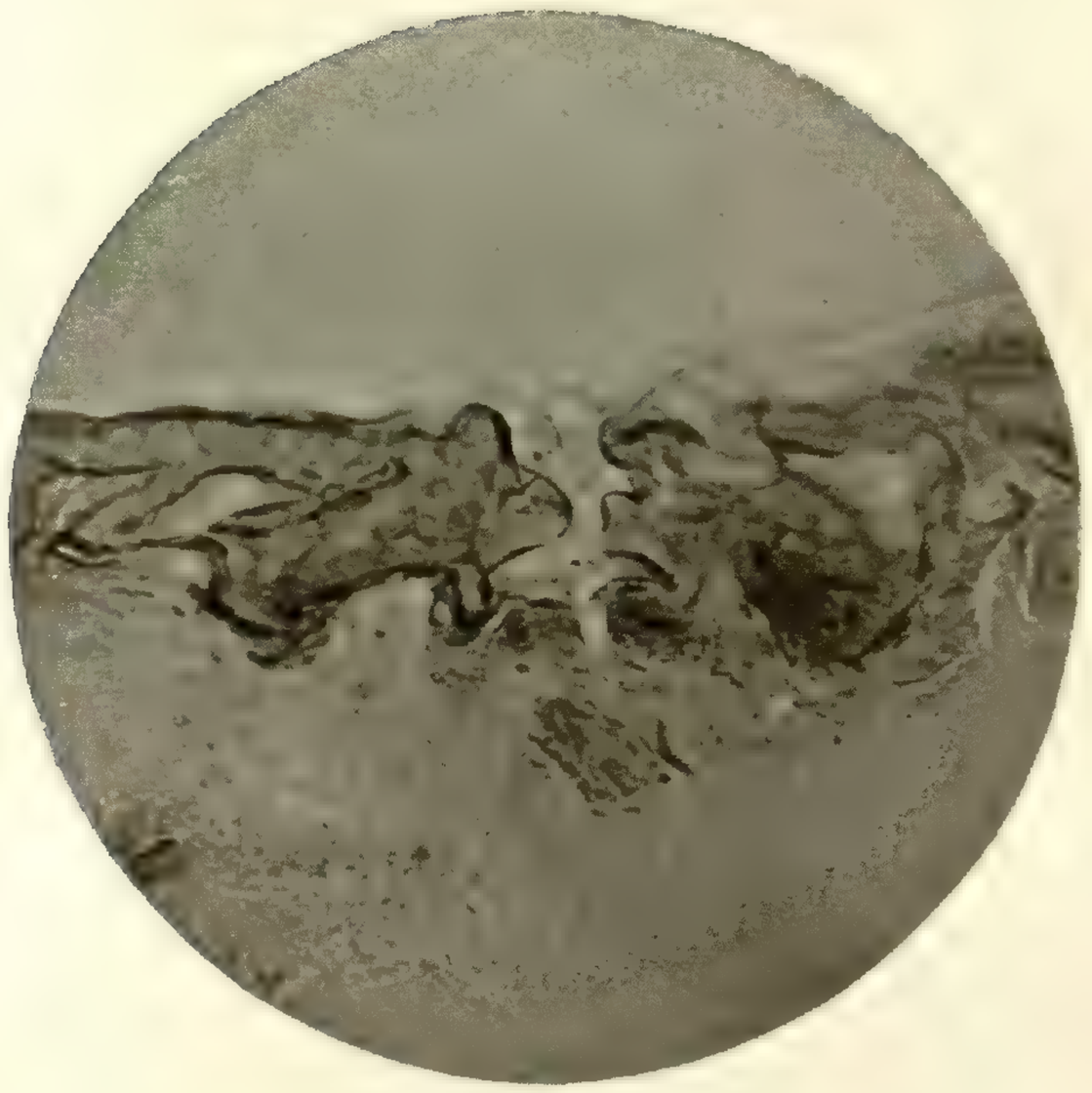

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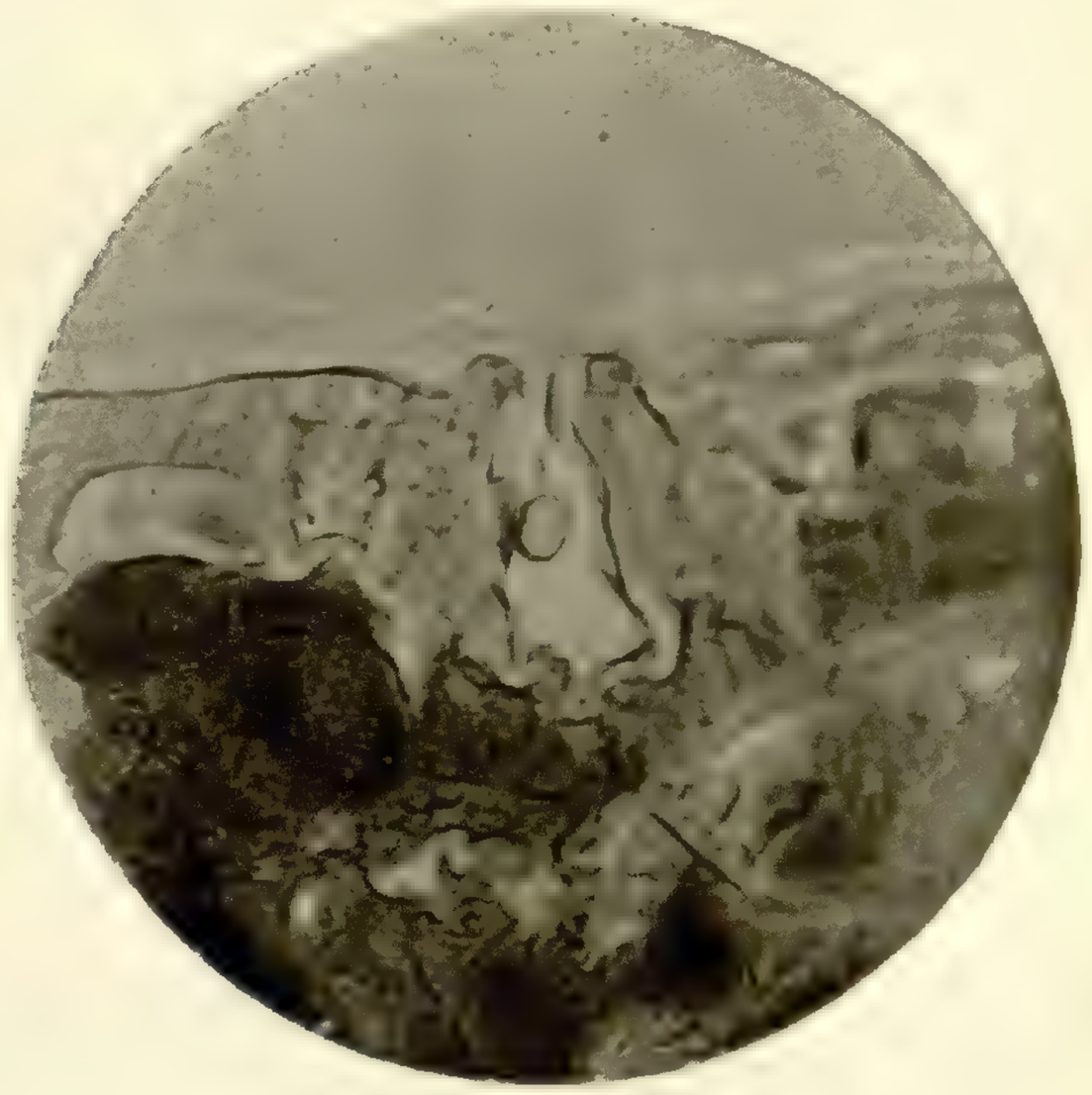

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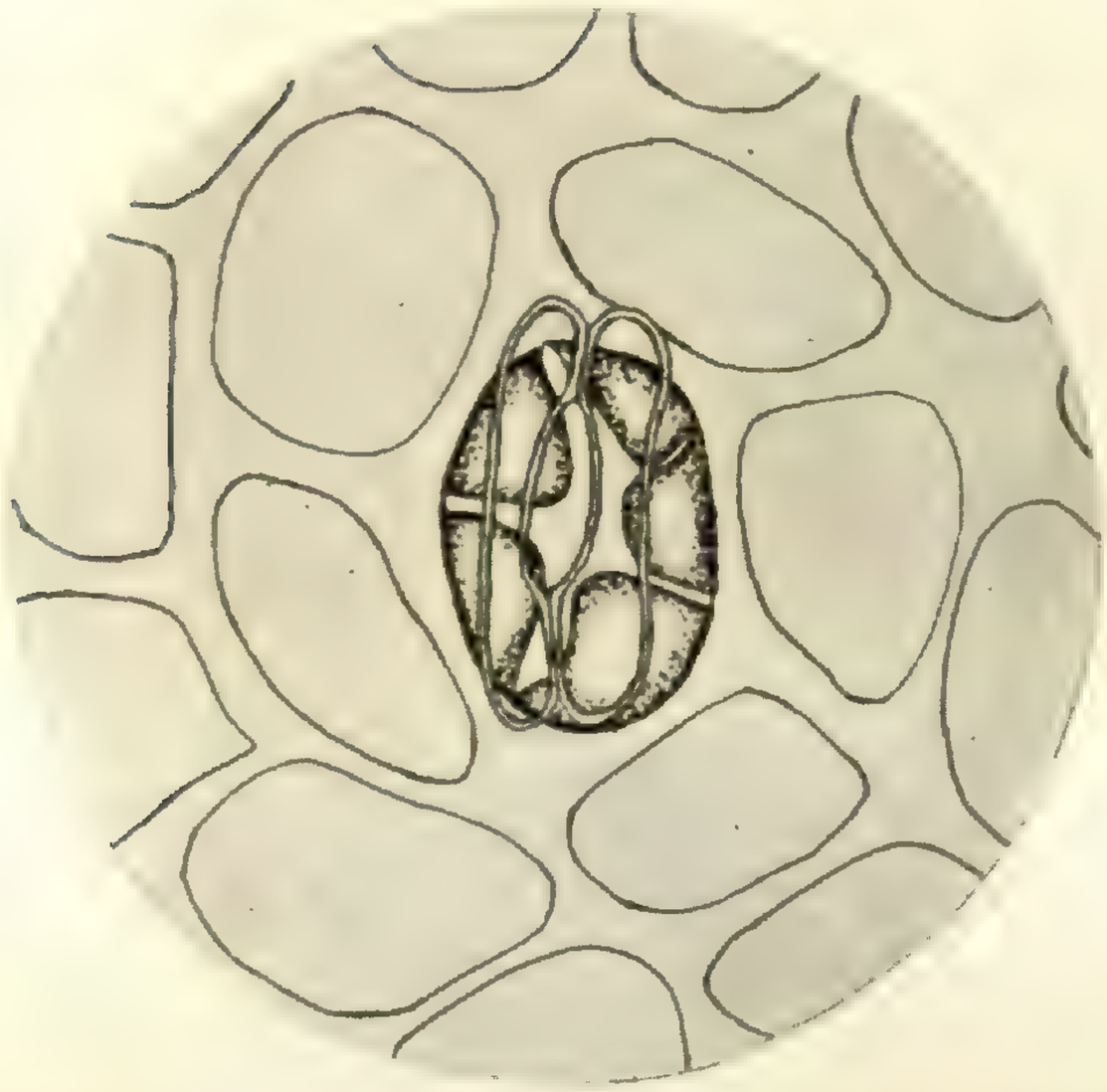

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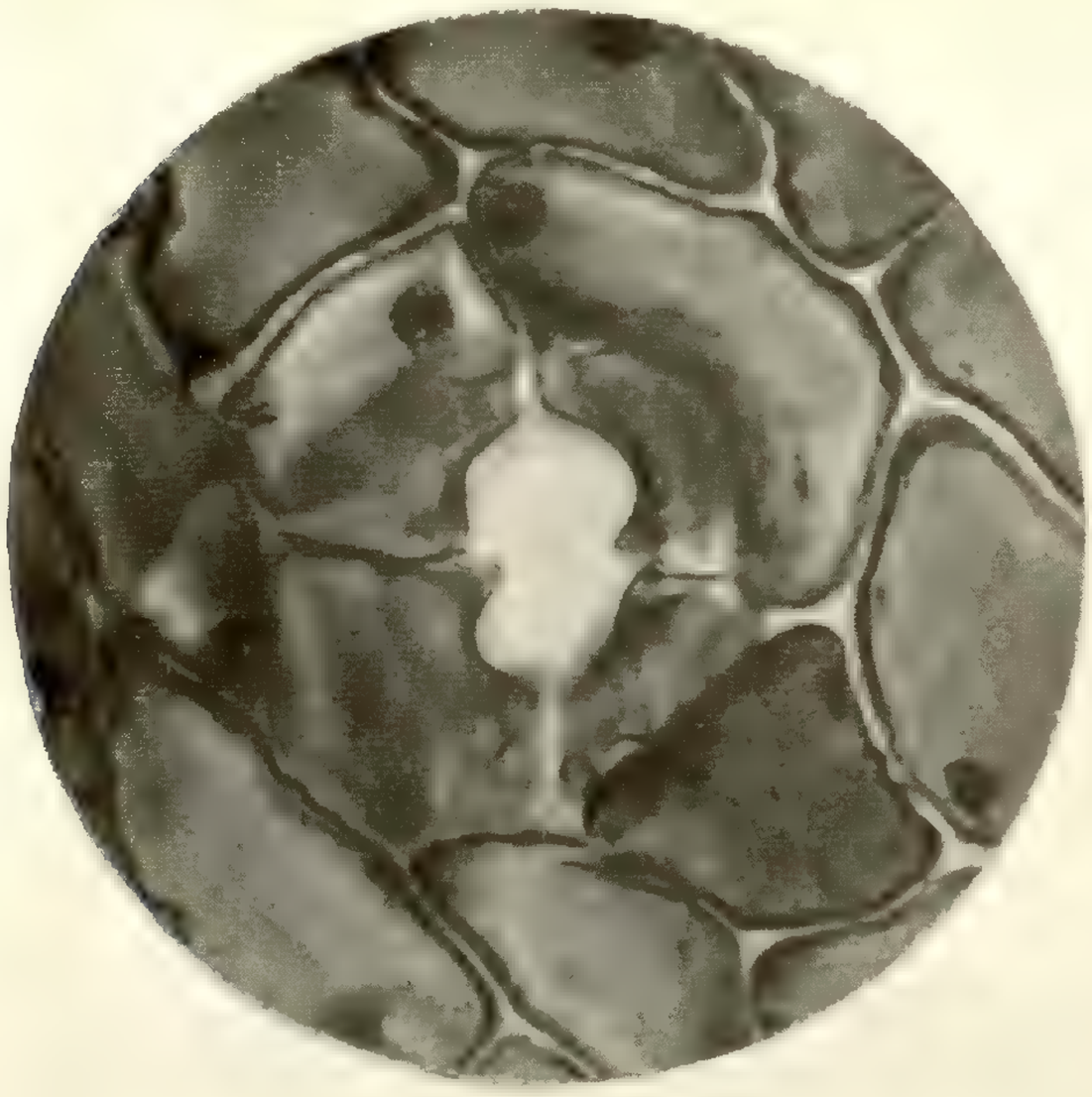

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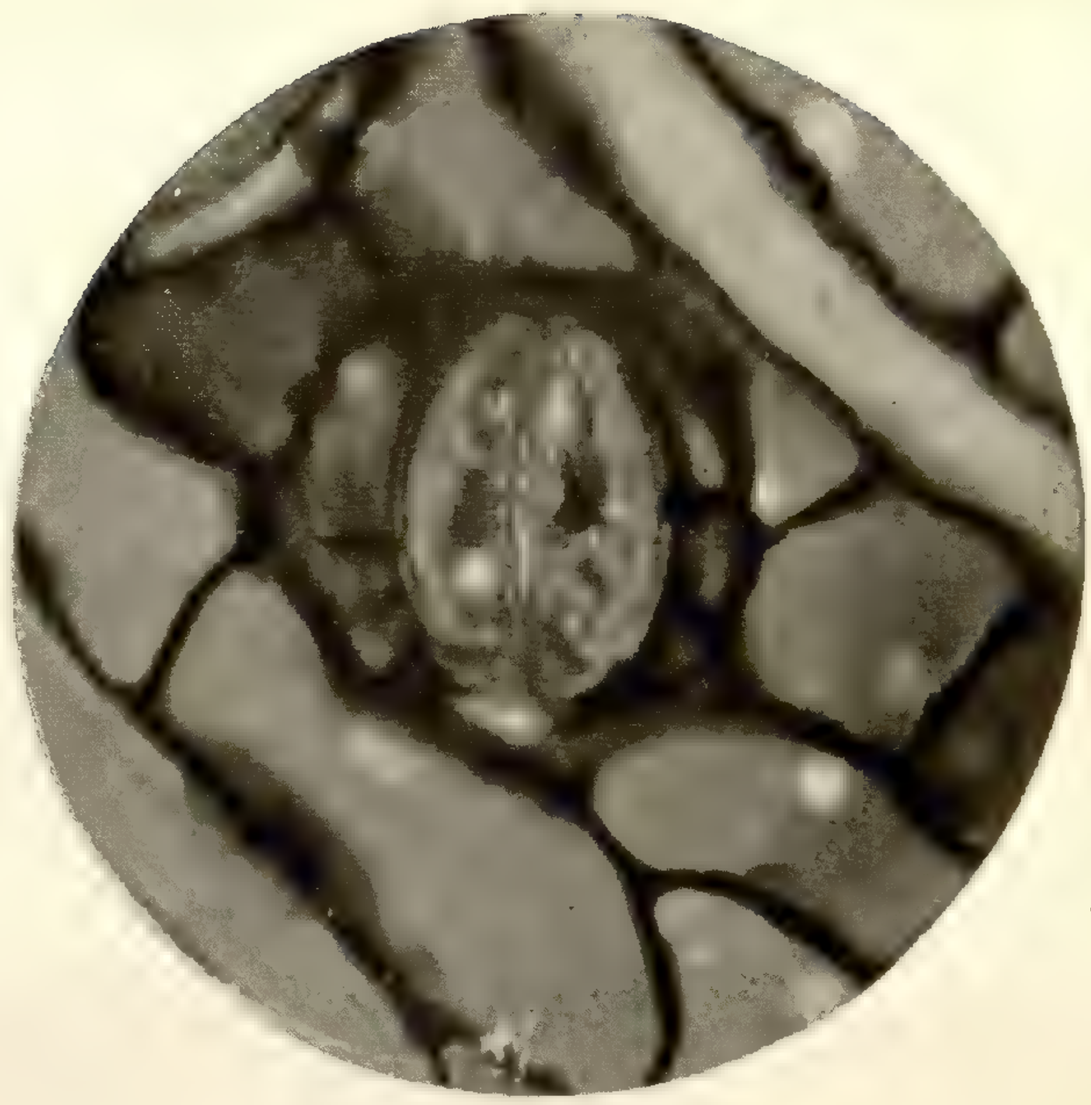

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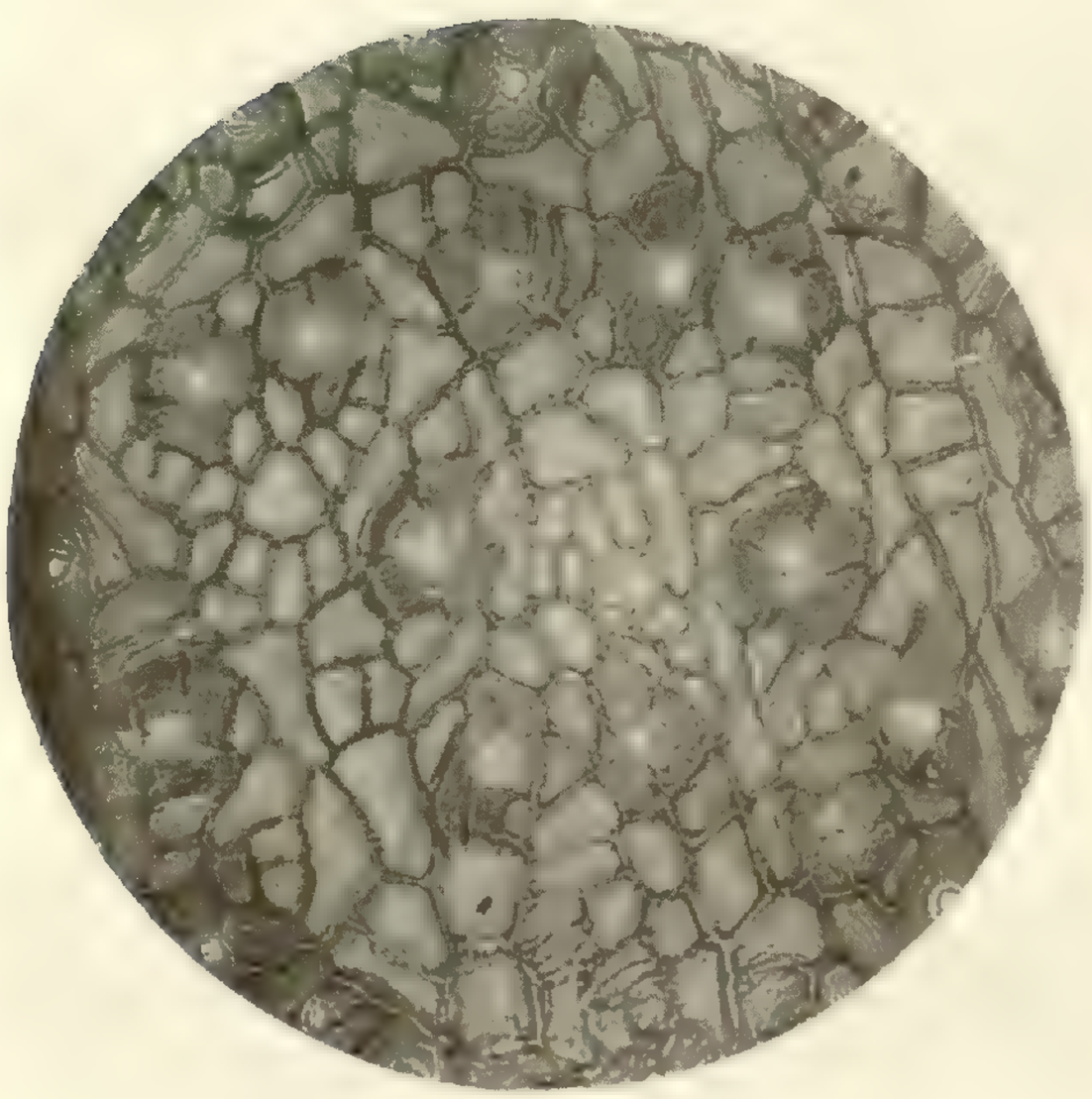

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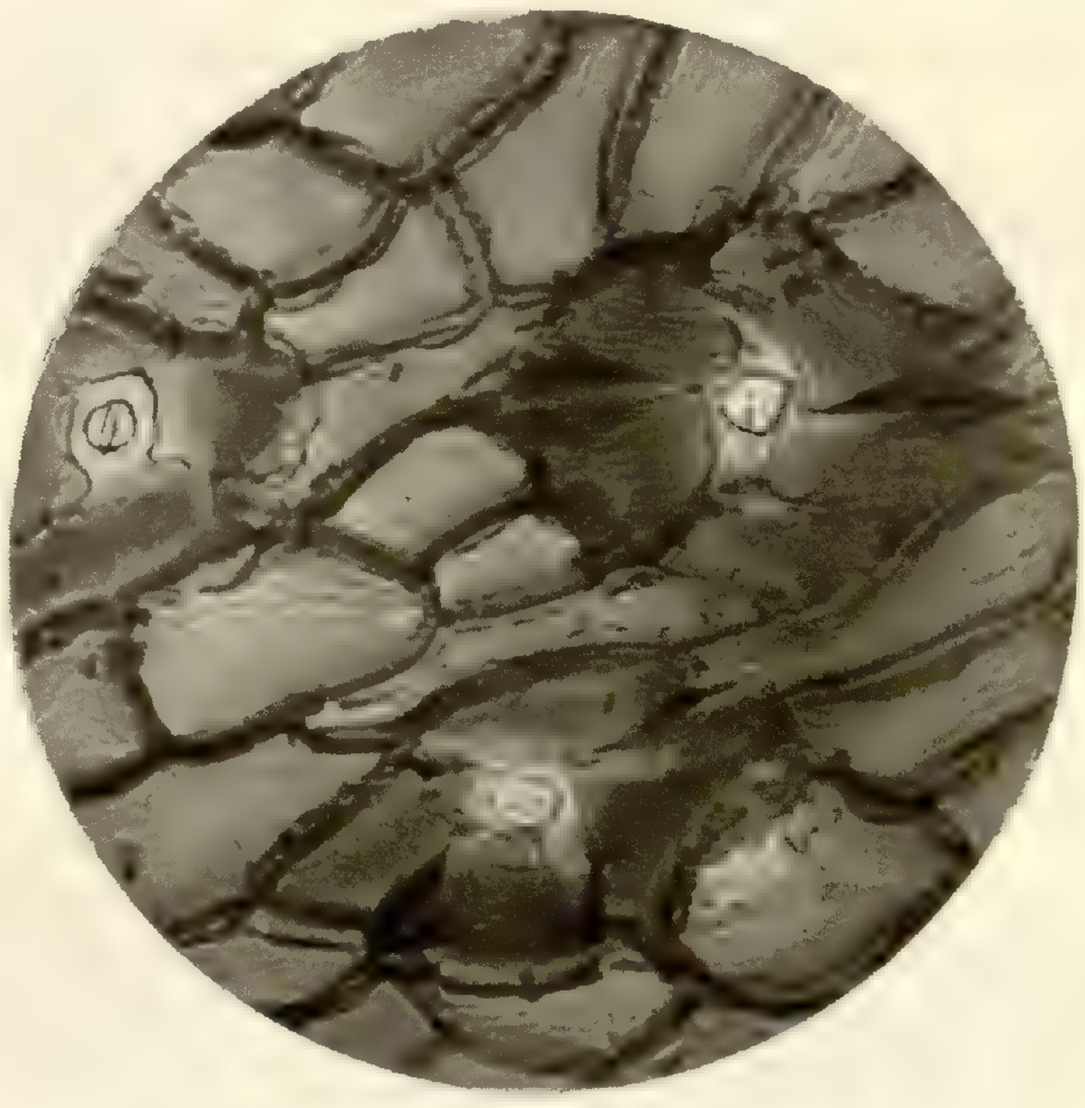

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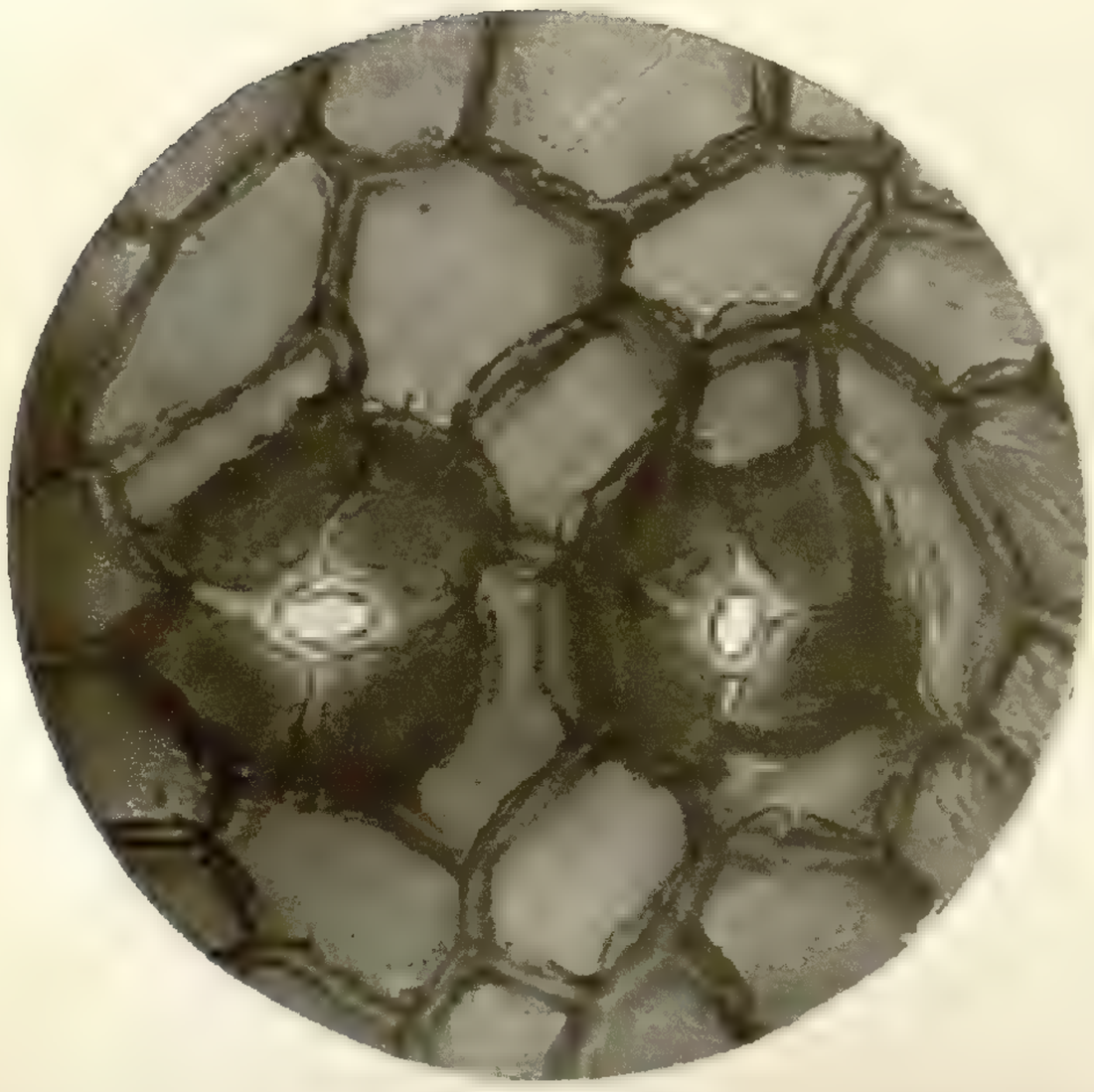

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so-called guard cells are really the commonly occurring accessory cells. The only recorded exception to the remarkably uniform organization of the stoma in the Embryophyta thus disappears.

The writer is indebted to Professor JEFFREY for the material used in this investigation, which was carried on under appointment as an 1851 Exhibition Science Research Scholar of the University of Toronto.

HARVARD UNIVERSITY
CAMBRIDGE, MASS.

EXPLANATION OF PLATES V AND VI

FIG. 1.—*Frenelopsis occidentalis:* stoma in surface view, showing the rosette of projections; ×333.

FIG. 2.—The same: vertical section through a stoma, showing the projections into stomatal cavity; ×250.

FIG. 3.—The same: vertical section of another stoma, showing two guard cells below the accessory cells; ×250.

FIG. 4.—The same: another stoma with distinct guard cells; ×250.

FIG. 5.—The same: camera lucida drawing of stoma from beneath, showing two guard cells above the accessory cells.

FIG. 6.—*Agathis bornensis:* vertical section of base of leaf, showing two guard cells sunken beneath conspicuous accessory cells; ×333.

FIG. 7.—The same: section parallel to the surface, showing stomatal opening surrounded by four accessory cells; ×333.

FIG. 8.—The same: section parallel to the last but deeper—below the accessory cells and including the two guard cells; ×333.

FIG. 9.—*Androvettia statenensis:* surface view of epidermis; ×63.

FIG. 10.—The same: higher magnification, showing two guard cells below accessory cells; ×250.

FIG. 11.—The same: stomata from which the guard cells have disappeared; ×250.

FIG. 12.—*Brachyphyllum macrocarpum:* section parallel to the surface, showing accessory and guard cells; ×125.

BRIEFER ARTICLES

EDUARD STRASBURGER[1]

(BORN FEBRUARY 1, 1844; DIED MAY 19, 1912)

(WITH TWO PORTRAITS)

In the death of STRASBURGER, professor of botany in the University of Bonn, science has lost one of its greatest investigators. His publications, extending over nearly half a century, naturally give the impression that he was a very old man, but such was not the case, for he was only in his sixty-ninth year, and was still actively engaged in research and teaching, when the end came suddenly through an attack of heart disease.

STRASBURGER was a native of Russian Poland, and began his education at Warsaw, studying later at Bonn and at Jena. He traveled extensively in Europe, and in 1873, with HAECKEL, he visited Egypt and the Red Sea, but most of his vacations were spent in Italy, on the Riviera. His wife died several years ago, but his children survive him. He was devoted to his family, was proud of his children, and during the long period while Mrs. STRASBURGER was an invalid, he always found time to accompany her in her daily walk through the beautiful gardens of the old Poppelsdorfer Schloss, once the palace of the Electors of Cologne, but now serving as the botanical laboratory and home of the professor of botany. With others also he was kindly and easy to approach, so that

[1] An account of STRASBURGER'S laboratory and work, written by Professor J. E. HUMPHREY, was published in this journal eighteen years ago (BOT. GAZ. **19**: 401–405, with portrait. 1894).

his students found in him not only a teacher, but also a sympathetic friend, interested in their researches, but also interested in their welfare after leaving his laboratory.

His first publications dealt with the embryology of gymnosperms, then with the more minute details of the life-history of angiosperms. In these researches he showed a profound grasp of the fundamentals of comparative morphology and gradually turned more and more to the study of the cell, until his laboratory became recognized as the most important cytological center in the world.

He was a remarkable lecturer. Although a master artist, he seldom used the chalk, but presented his subject in such vivid word pictures that any further illustration seemed unnecessary. His usual lectures to students covered morphology from the algae to the flowering plants, and every Friday he gave a lecture, open to the public, upon some botanical subject of popular interest.

In the research laboratory he visited every student every day, and always had some helpful suggestion or criticism, but the student would learn on the first day that STRASBURGER had no time to waste. This daily round, in which he might visit as many as eight investigators, seldom occupied more than half an hour, but occasionally, after the usual laboratory hours or on Sundays, he would come into the laboratory, when only one or two students were present, and talk familiarly on various subjects for an hour or more. He seemed particularly attached to his American students. It was my privilege to know him rather intimately at Bonn, and during the ten years which have elapsed since my return, a constant correspondence has continued the inspiration and helpfulness received while at his laboratory. Some quotations from this correspondence will be of more interest than anything else one could write. In a letter of June 29, 1910, he says: "I prize very highly the kindly recogni-

tion of my scientific efforts by my American colleagues. It is a great pleasure to note the tremendous advances of our science in the United States, and to be able to say to myself that in some measure I have been responsible for it."

Of the greatest interest is a letter of October 2, 1908, written in response to a request for some data to be used in an historical seminar at the University of Chicago.

LIEBER HERR KOLLEGE:

You overestimate my contributions! I myself am inclined to believe that I have often failed and only in part attained the scientific ideal which hovered before me. However, in the investigation of life everything is still in flux, the solution of the problems lies in the distant future, and the best that can be said of any one of us is that he was a necessary stage along the way to knowledge. What gratifies me particularly is that in my lecture-room and laboratory I have inspired competent, gifted men of high ideals to strive for the same goal which hovers before me, and that my work shall continue to live in theirs.

Since you wish to know it, I was born on February 1, 1844. I studied first at Bonn, where I gained technical skill under HERMANN SCHACHT, and at the same time found a great stimulus in the lectures of JULIUS SACHS, who at that time was a teacher in the Poppelsdorf Agricultural Academy. The sudden death of SCHACHT made me decide to go to Jena to PRINGSHEIM, who had met me in his visits to SCHACHT, and who invited me to become his assistant. The critical mind of PRINGSHEIM reacted beneficially upon me, while my association with ERNST HAECKEL soon made me enthusiastic over the great problem presented by CHARLES DARWIN.

My acquaintance with my ten years older teacher soon became friendship, and I have to thank ERNST HAECKEL that two years after my promotion in Jena, when PRINGSHEIM retired, I was called to his place. I was then 25 years old. I was never closely associated with HOFMEISTER. Unfortunately, during the latter part of his life, HOFMEISTER became very sensitive and was angry with me because in 1869 in my work on *Befruchtung bei den Coniferen* I sought to prove that the "corpuscula" do not correspond to the embryo sacs of angiosperms, but are archegonia. HANSTEIN came to Bonn as professor after I had already settled in Jena. In 1887 I came to Bonn as HANSTEIN'S successor. I had been teaching in Jena for twelve years.

With hearty greeting, your very devoted,

E. STRASBURGER

In his correspondence with his colleagues, STRASBURGER never used a typewriter, feeling that a typewritten letter indicated haste and lack of respect. The following is a reproduction, slightly reduced, of a noble paragraph from the above letter.

—Was mich trotzdem freut, ist aber dass ich, in meinem Vorlesungsraum und Institut, tüchtige und begabte, ideal angelegte Männer für die hohen Ziele die uns selber vorschweben, zu begeistern wusste und dass meine geistige Arbeit in ihrer Arbeit fortleben wird

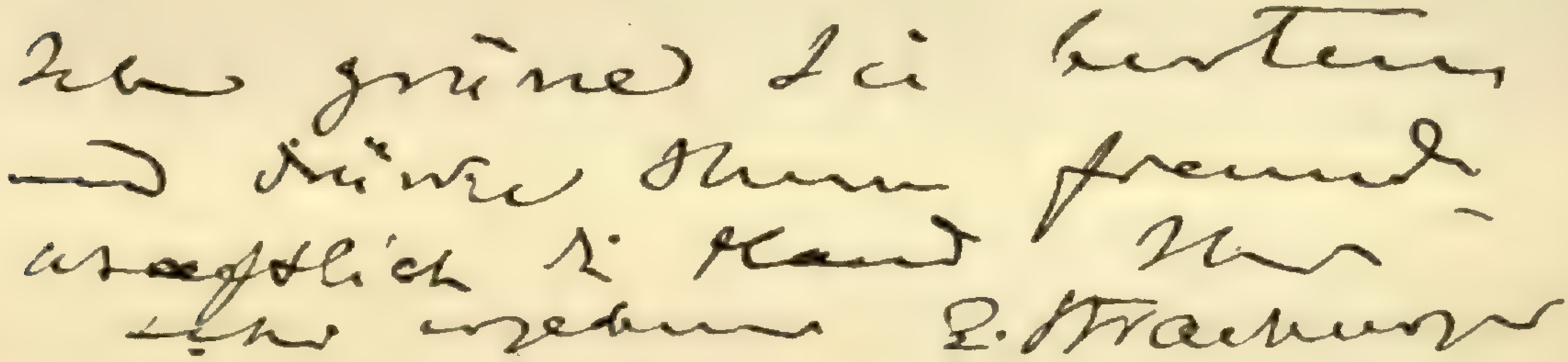
STRASBURGER felt keenly the attack made upon him on account of his paper on graft hybrids. He felt it beneath his dignity to reply, but in a letter of January 6, 1910, he says: "I had the position to defend which I have held in regard to the rôle of the nucleus in fertilization and heredity, and which WINKLER threatened to overthrow. That alone was responsible for my paper in the *Berichte der deutschen botanischen Gesellschaft*."

For some time he had known that his health was failing, but he had continued to work, and his publications show that he was still in his prime and that advancing years had only brought their experience and power without weakening his initiative or enthusiasm in research. At the time of his death, he was deeply interested in the problem of the determination of sex and had investigations under way bearing upon this important subject, but was being delayed by another piece of work. In a letter of March 5, 1911, he writes:

Unfortunately, I have not got to my microscopic work this winter. A year ago I saw myself necessitated to take part in a scientific publication of pretentious scope, bearing the name *Kultur der Gegenwart*, which is to present in accessible form the whole field of science. The plan may be good in itself, but I have often deplored that I allowed myself to undertake the work and that I must devote to it, rather than to my own research, the few years of scientific activity which still remain for me. Besides, I have not felt well this winter,

and in spite of the advice of my physician, have had to work hard. Day after tomorrow I start for the Riviera and shall see whether I may not recuperate a little.

At the present time a *Festschrift* is under way to commemorate STRASBURGER'S seventieth birthday. A complete account of his life and work will doubtless be published, but a brief notice is appropriate at this time, and the words from his own pen will be appreciated by his numerous pupils and friends. The photograph taken in his regalia, while he was president of the University of Bonn, was given with the injunction that it must not be shown in Germany nor published anywhere during his lifetime. The other photograph was taken in 1892.



—CHARLES J. CHAMBERLAIN, *The University of Chicago*

CURRENT LITERATURE

BOOK REVIEWS

The Chicago textbook[1]

Of the three parts composing the Chicago *Textbook of Botany for Colleges and Universities*, "Morphology" by COULTER and "Physiology" by BARNES appeared nearly two years ago, and were noticed in this journal[2], while "Ecology" by COWLES, concluding the work, appeared in January and is now before us.

However eagerly parts I and II were anticipated by all concerned with botanical education, an even warmer welcome has been ready for part III, because, while the former had predecessors, the latter has not. What, then, are the characteristics of this first compendious textbook of ecology? In the first place, as most botanists will notice with pleased surprise, the book is primarily a description and analysis of the ecological factors, treated in connection with the principal organs—roots, stems, leaves, etc.—with which they are most closely associated; while the synthetic phases of the subject—those discussions of associations, formations, societies, etc., which have to come to stand in the minds of most people as synonymous with the very word ecology—are relegated to a single brief chapter. This is wise, because it is becoming quite plain that the relative barrenness of synthetic ecology is a natural consequence of the newness, crudeness, and deficiencies of our knowledge of analytical ecology. In the second place, the book is a remarkably clear and forceful presentation of its subject, the exposition, indeed, being in no wise inferior to the high standard of the preceding parts, while occasional important passages (e.g., the description of photosynthesis on pp. 525–526) are notably effective. Furthermore, a striking quality of the book is completeness, but it is a question whether in this feature a virtue has not been carried so far as to constitute a fault; for so detailed is the treatment, and so obvious is the intention to leave no important phase of the subject untouched, that the work is carried out of the field of the textbook, in which rigid selection and proportion are essential, into that of the handbook, where completeness is of course a very first requisite. This view receives incidental confirmation from the length of this part in comparison with the others, for it comprises no less than 479 pages, as contrasted with the 296 of part I, which covered all of morphology,

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[1] COULTER, BARNES, and COWLES, A textbook of botany. Vol. II. Ecology. 8vo, pp. 480. *figs. 535*. New York: American Book Co., 1912. $2.00.

[2] BOT. GAZ. **51**:67. 1911.

including the whole range of the groups, and the 189 of part II, which comprised all of physiology. So gross a relative disproportion between bulk and intrinsic content value, while unjustifiable from the textbook point of view and prohibitive of the acquisition by a student of any such clear-cut and well proportioned view of its subject as parts I and II afford, is perhaps allowable on the ground of the genuine need for a first formulation of the material. In the third place, the book displays the same wealth of well selected illustration, and the same tasteful, even beautiful typography of the earlier parts. And finally, so far as the accuracy of the fact-matter is concerned, it will require a vastly larger knowledge of the material than the present reviewer possesses to detect any considerable error either of statement or omission, while such flaws as appear are too insignificant for mention. It is, in brief, a distinctive, authoritative, foundational work, destined to take an immediate place as an indispenable reference work for all concerned with the life-phenomena of plants.

A remarkable feature of the book consists in its philosophy. This may be summarized as a systematic antagonism to everything Darwinian. Under the assumption that the language commonly in use to describe the relations of plants to their surroundings, including such words as adaptation, adjustment, storage, etc. (p. 487), mislead learners into a belief that plants act with an even more than human forethoughtfulness (p. 950), the author attempts to avoid all such expressions, visiting with especial condemnation anything of teleological implication. But only a bogey of his own creating is at the bottom of the author's trouble. No students, in the reviewer's experience, if only half-decently instructed, ever gather any such notions. Besides, Darwin himself, as to whose views, of course, there is difference of opinion, but as to whose rationalistic habit of mind there is none, habitually uses teleological language throughout his works without ever having been misunderstood in this respect. However, Professor COWLES is apparently not an evolutionist, because, after expressly and repeatedly combating the idea of a historical or causative adaptation, which he makes either an accident or a psychological illusion, he replaces it by the idea of "mechanical causation" (p. 487), that is, passive reaction to mechanical, physical, or chemical influences. Now this idea carries the inevitable corollary that such responses must be always the same in the same part under the same conditions, and that therefore they cannot be modified into anything else, any more than chemical compounds can change the nature of their reactions to outside influences; and without such possibility of change, no evolution, but only a kind of spontaneous creation, is possible. In his opposition to everything savoring of adaptation, the author is led at times even to a distorted representation of the views he opposes. Thus, no authors, that the reviewer can recall, and certainly none of authoritative rank, have ever maintained any such naïve conception of adaptive response as is attributed to some of them, by implication, at the top of p. 950. Indeed, the author's view of everything relating

to adaptation is distinctly myopic, and the treatment of those subjects tends to the dogmatic, not in language but in spirit. This very book seems to the reviewer to show that whatever the deficiencies of the adaptation-selection hypothesis, it still has to its credit a notable balance of reasonableness in comparison with the proposed substitute.—W. F. GANONG.

An elementary text

A new elementary text by BERGEN and CALDWELL[3] attempts to meet the growing demand for practical botany, which means the economic aspects of plants. This demand arises not only from the interest of pupils in the "bread and butter" side of science, but also from what is thought to be the greatest need of that very large proportion of high-school students whose formal education ends with the high school. There is no question that advantage should be taken of interest and need, and the only question is as to whether they are satisfied by a proposed course of study. Moreover, this question can be answered only by experience. Many a public demand voices a real need, and then the change comes to stay; and many another public demand voices an imaginary need, and then the change soon passes into the limbo of "fads."

The book before us has been handicapped in setting the task of meeting a possible public need and at the same time meeting the artificial need of entrance requirements imposed by colleges. As a result, the unifying motive is lacking and the book becomes a mosaic rather than a definite pattern. The field of previous texts is covered, and to this is added the economic phases of plants, which compels a brevity of treatment in many cases that results in obscurity. In spite of the divergent purposes and space limitations, the book is a marked advance in the direction intended.

Some of the noteworthy features are: an introductory general survey of plants in relation to man, and "the plant as a working unit" (pp. 23); elementary forestry (pp. 21); plant breeding (pp. 21); plant industries (pp. 30); weeds (pp. 11); leading families of flowering plants and their uses (pp. 35); and especial emphasis upon plant diseases and methods of control. In a practical botany of 513 pages, one is surprised to find no less than 214 pages devoted to plant groups. However, economic significance has frequently determined the selection of the forms discussed. With the exception of most of the material treated under "The great groups of plants" (pp. 156–370), the text has a decided flavor of elementary agriculture and might well serve as a text in elementary agricultural botany, though such an important topic as seed testing and selecting is conspicuous by the absence of any special treatment. The numerous footnotes and references to literature should prove both useful and stimulating, at least to instructors. The introduction of

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[3] BERGEN, J. Y., and CALDWELL, O. W., Practical botany. pp. v+545. *figs. 381.* Boston: Ginn & Co., 1911.

numerous new and well chosen cuts is refreshing. Unquestionably the book is a valuable addition to elementary texts in botany and should find a wide field of usefulness in the hands of trained instructors.—LEROY H. HARVEY.

MINOR NOTICES

Nature sketches.—The chief scientific value of HANCOCK'S *Nature Sketches*[4] is the large number of accurate and original observations upon insects and other animals in relation to their natural environments. The first chapter contains an unusually clear and simple discussion of problems and theories of evolution. Insect and bird pollination, and the relations of animals to flowers are discussed and beautifully and accurately illustrated, especially in the second chapter, by drawings, photographs, and colored plates of examples from temperate America. The adaptations of insects, birds, and flowers are discussed, and the author appears to be of the opinion that everything is useful. It is unfortunate that the idea of adaptation should be introduced without qualification into a popular work at a time when many botanists and zoologists regard it as doubtful. The chapters on "Animal behavior" and "Ecology" should have had less comprehensive titles. Though somewhat confused with faunistic geography, the first five pages of the chapter on ecology are devoted to a good summary of some of the important facts of genetic ecology. The lists of plant and animal habitats at the end of the book give the habitat preferences of a number of Orthoptera, but contain few elements of progress in ecological classification. The current classification has not been followed.[5] In addition to its scientific value, the book is a good introduction to many aspects of natural history for the lay reader.—V. E. SHELFORD.

Popular manuals.—The nature and purpose of the very interesting *Cambridge manuals of science and literature* have been noticed in this journal.[6] At that time five volumes dealing with plants had been published, and now two additional volumes have appeared: *Links with the past in the plant world*, by A. C. SEWARD (pp. 142); *Life in the sea*, by J. JOHNSTONE (pp. 150). The volumes are sold for one shilling each, and form for the general reader a readable résumé of current scientific knowledge. The titles of the eight chapters of Professor SEWARD'S volume will give a better conception of the contents than does the general title. They are as follows: "Longevity of trees, etc."; "The geographical distribution of plants"; "The geological record"; "Preservation of plants as fossils"; "Ferns, their distribution and antiquity"; "The redwood and mammoth trees of California"; "The Araucaria family";

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[4] HANCOCK, JOSEPH L., Nature sketches in temperate America. 8vo. xviii+451. *pls. 12. figs. 215.* Chicago: A. C. McClurg & Co. 1911. $2.75.

[5] PEARSE, in Science **34**:37. 1912, is mistaken in this matter.

[6] BOT. GAZ. **52**:234. 1911.

"The maiden hair tree." The American publisher is G. P. PUTNAM'S SONS of New York.—J. M. C.

North American Flora.[7]—Vol. VII, part 3, continues the treatment of the Uredinales and contains the Aecidiaceae from *Prospodium* to *Dichaeoma* by JOSEPH CHARLES ARTHUR, the text for the genus *Gymnosporangium* being contributed by FRANK DUNN KERN. One new genus (*Argomyces*) is proposed, which has a geographical distribution from New Mexico and Texas through Mexico and the West Indies to South America, and is represented at present by four known species. Further new species are characterized in the following genera: *Earlea* (1), *Kuehneola* (1), *Spirechina* (1), and *Xenodochus* (1).—J. M. GREENMAN.

NOTES FOR STUDENTS

Variation curves.—Several years ago papers dealing with variation in the number of parts of flowers, flower heads, inflorescences, etc., were of frequent appearance. As the novelty of the method disappeared, the number of contributors to the knowledge of such variations has decreased, but, as is usually true in such cases, the value of the contributions has correspondingly improved. Several recent studies in this field are of exceptional interest.

VOGLER[8] gives a large number of counts of ray flowers in *Chrysanthemum*, *Boltonia*, and *Senecio*. In *Chrysanthemum Parthenium* he found a curve having the mode on 21 when the plants were grown on well-manured soil, and on 13 when grown on infertile soil, the curves being strongly skew in each case toward an intermediate point, the mean values lying between 14 and 19. These results agree essentially, therefore, with those of KLEBS[9] on *Sedum spectabile*. In *Boltonia latisquama* the ray flowers have a wide range of variation (39–81), with the summit of the curve near 55. Three different plants were separately counted in three successive years, and although the different seasons differed considerably, there was no corresponding change in the number of ray flowers. One of these plants had each year the mean number approximately 57, another approximately 54. These permanent differences are probably not to be attributed to genotypic differences in the plants, however, as they originated from a common stock by vegetative division. In *Senecio alpinus* a count of over 3000 heads from two different localities in three different years gave in every case a nearly monomodal curve with the mode on 19, thus convincing the author of the limitations of Ludwig's law that the maxima of such

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[7] North American flora. Vol. VII, part 3, pp. 161–268. The New York Botanical Garden. April 15, 1912.

[8] VOGLER, P., Variation der Anzahl der Strahlblüten bei einigen Kompositen. Beih. Bot. Centralbl. **25**:387–396. 1910.

[9] KLEBS, G., Studien über Variation. Arch. Entwick.-Mech. Organ. **24**:29–113. 1907.

variation curves fall upon the numbers of the Fibonacci series, 2, 3, 5, 8, 13, etc., and low multiples of them, or on the similarly constituted "Trientalis-series," 3, 4, 7, 11, etc., and their low multiples. The latter series was discovered by LUDWIG in *Trientalis*, whence its name. VOGLER[10] had found earlier that the modes in the number of umbellary rays of *Astrantia major* fall upon members of the Fibonacci series when only the primary umbels are included, but in the secondary umbels the modes are on the Trientalis series. More recently the same author[11] has reported on the number of ray flowers in *Arnica montana*, *Buphthalmum salicifolium*, *Eupatorium molle*, *Aster novi-belgii*, *Senecio erucifolius*, and *Chrysanthemum Parthenium*. Several of these species gave well-marked modes on the Fibonacci numbers, but in other collections of data from the same species the mode occurred not infrequently on some quite unrelated number. For example, in *Arnica montana* a collection from Rigi, Switzerland, in 1908, showed modes on 13, 16, and 21, while heads of the same species collected the next year at Klosters presented a well-developed mode on 11 and only a slight indication of a mode on 13. Later analysis of this case showed that the terminal heads give modes on 13 and 16, while secondary heads give modes on 11 and 14, the latter numbers bearing the same relation to the Trientalis series that the former do to the Fibonacci series. This whole problem as to the position of the modes in variation curves of ray flowers, and other organs which are related more or less definitely to the phyllotactic spiral, is still unsolved, though it is evident that the Fibonacci series supplies the modal numbers in many cases, and that other equally definite series are followed in other cases. It is very rare that the number of variates used by investigators is sufficiently great to establish with any considerable degree of probable correctness these relatively superficial features of the curves. RITTER has gone to the length of asserting that non-phyllotactic variates among plant organs have their modal numbers also related to the Fibonacci or Trientalis series. He even contends that this is true of graduated variates. In support of this view he tabulates[12] a rather meager series of measurements of width and length of leaves and leaflets of *Stellaria media*, *Oxalis Acetosella*, *Lysimachia nummularia*, *Hypericum perforatum*, *Caragana arborescens*, *Rosa canina*, *Medicago sativa*, *Symphoricarpus racemosus*, *Fragaria vesca*, and *Cytisus Laburnum*, and the width and length of fruits of *Alnus glandulosa*, *Rosa canina*, *Quercus Robur*, and *Q. sessiliflora*. He believes that the measurements of surfaces, such as leaf blades, give modes related to the square roots of the Fibonacci numbers, namely, on $10\sqrt{1}$, $10\sqrt{2}$, $10\sqrt{3}$, $10\sqrt{5}$, $10\sqrt{8}$, etc.,

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[10] VOGLER, P., Variationstatistische Untersuchungen an den Dolden von *Astrantia major*. Beih. Bot. Centralbl. **24**: 1–9. *figs. 6.* 1908.

[11] VOGLER, P., Neue variationstatistische Untersuchungen an Compositen. Jahrb. St. Gallischen Naturwis. Gesells. 1910: 1–32. 1911.

[12] RITTER, G., Über discontinuirliche Variation im Organismenreiche. Beih. Bot. Centralbl. **25**: 1–29. 1909.

and that in tri-dimensional material such as fruits, the modes are related in similar manner to the cube roots of the Fibonacci numbers. The absurdity of such a view will be obvious when it is considered that nature takes no note of such arbitrary units of measure as the millimeter and centimeter, and that the choice of any other unit of measure would place the modes on other values. VOGLER[13] shows by a much more extensive series of measurements of leaflets of *Cytisus Laburnum* that while the curves are multimodal, the modes can not by any sort of manipulation be made to fit the Fibonacci series.

In another paper, VOGLER[14] performs an important service by summarizing the statistical studies which have been made upon the heads of Compositae and the umbel rays of the Umbelliferae, together with a few of the more important investigations upon the flowers and inflorescences of other species. The list of Compositae includes 45 species and of the Umbelliferae 10 species. The list gives not only the names of the species and the particular organs studied, but also states the number of counts upon which conclusions regarding the several species have been based, the apparent modes, and references to papers in the appended bibliography in which the results are recorded. This bibliography contains 63 titles.

DE BRUYKER[15] makes an extensive study of variation in the umbels of *Primula* the motive for presenting a discussion of the entire subject of statistical variation. This simple and concise presentation of the subject should occupy for Dutch readers a place similar to that held by JOHANNSEN'S[16] discussion for readers of German. It is not necessary here to consider the general treatment of the subject of variation as given by DE BRUYKER, but only the new results relating to *Primula officinalis*, *P. farinosa*, and *P. elatior*. The modal numbers of flowers in the inflorescences of these three species fall with considerable regularity upon the numbers of the Fibonacci series, but collections taken at different parts of the season show a gradual decrease in the average number of flowers per inflorescence as the season progresses. Plants growing in a favorable environment had the mode on 5, and in less favorable ones on 3. The similarity of results in collections from good and bad surroundings, and in early and later parts of the season, convinces the author of the correctness of the interpretation of the gradual fall in mean number of parts during the

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[13] VOGLER, P., Die Variation der Blattspreite bei *Cytisus Laburnum* L. Beih. Bot. Centralbl. **27**: 391–437. *figs. 12*. 1911.

[14] VOLGER, P., Probleme und Resultate variationstatistischer Untersuchungen an Blüten und Blütenständen. Jahrb. St. Gallischen Naturwis. Gesells. 1910: 33–71. 1911.

[15] DE BRUYKER, C., De statistische methode in de plantkunde en hare toepassingen op de studie van den invloed der levensvoorwarden. pp. 226. *figs. 33*. Gent: A. Siffer. 1910.

[16] JOHANNSEN. W., Elemente der exakten Erblichkeitslehre. pp. vi+516. *figs. 31*. Jena: Gustav Fischer. 1909.

season, which attributes it to a change of nutrition, an interpretation which was given independently by MACLEOD and the reviewer about ten years ago. The polymorphism shown by the multimodal curves is interpreted by DE BRUYKER as due to differences in nutrition acting in conjunction with a discontinuous mode of development, through which the new organs tend to be added in groups instead of singly. The same explanation or one essentially similar is applicable to other multimodal variation curves, the series of modes being determined by the manner in which each succeeding group of organs added is related to the preceding group or groups.

DE BRUYKER recognizes nine series of modes for multimodal variation curves. These are as follows: (*a*) the powers of 2 (2, 4, 8, 16, etc.), as in the peristome teeth of mosses; (*b*) multiples of 3 (3, 6, 9, 12, etc.), as number of flowers in *Lonicera caprifolium;* (*c*) multiples of 4 (4, 8, 12, 16, etc.), as in the number of flowers per umbel in *Cornus Mas;* (*d*) multiples of 5 (5, 10, 15, 20, etc.), as in the number of stamens in *Pyrus communis;* (*e*) the Fibonacci-Ludwig series (1, 2, 3, 5, 8, [10], 13, [16], etc.), as in many Compositae, Umbelliferae, etc.; (*f*) the Trientalis series (1, 3, 4, 7, 11, 18, etc.), as in *Trientalis*, secondary umbels of *Astrantia major*, lateral heads of *Arnica*, etc.; (*g*) Cardamine series (2, 5, 8, 11, 13, 16, 19, 22), as found by VOGLER for the number of flowers in *Cardamine pratensis;* (*h*) the odd series (1, 3, 5, 7, 9, etc.), as in number of leaflets in imparipinnate leaves, etc.; (*i*) the even series (2, 4, 6, 8, etc.), as in paripinnate leaves, rows of grains on ears of maize, etc.

By selecting for higher number of rays in *Calliopsis bicolor*, under conditions of high nourishment, DE BRUYKER was able to secure a strain of this species, by far the largest number of whose heads had 13 rays, though the material with which he began selecting gave a very high percentage with only 8 rays. This result corresponds with that of DEVRIES with *Chrysanthemum segetum*. The sensitive period for the influence of nourishment on the number of ray flowers was investigated in *Chrysanthemum carinatum*, and this period was observed to close four or five weeks before the opening of the heads. DE BRUYKER's work closes with a succinct statement of the principal results of the author's investigations on *Primula elatior*, *Chrysanthemum carinatum*, *C. segetum*, *Calliopsis bicolor*, *Scabiosa atropurpurea percapita*, rye, barley, and wheat. The bibliography contains references to a few more than 100 papers dealing with the subject of variation and its statistical study, and a full index is added.

NIEUWENHUIS[17] has studied the changes in the variations and in the mean values of the number of ray flowers in nine species of Compositae from the beginning to the end of the flowering season. He finds in seven of these species an essential agreement with the behavior found by the reviewer[18] in *Aster*

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[17] NIEUWENHUIS, M., Die Periodicität in der Ausbildung der Strahlblüten bei den Kompositen. Recueil Trav. Bot. Néerl. **8:** 108–181. *figs. 23.* 1911.

[18] SHULL, G. H., Place-constants for *Aster prenanthoides*. BOT. GAZ. **38:** 333–375. 1904.

prenanthoides. The characteristic periodicity curve of mean values in these species rises quickly to a maximum in the early part of the season, after which there is a much more gradual decline until the end of the season. Only in *Melampodium divaricatum* and in *Cosmos sulfureus* was there no essential change throughout the season, the former species having a single mode on 10 with the mean slightly above 10 in every collection made, and the latter species presenting a similar constancy, having at all times a half-curve, falling steeply from a strong mode on 5 only to higher values. In most of these species the modes were on the Fibonacci numbers; and while the changes in mean values were gradual and continuous, the appearance of modes on intermediate numbers was relatively rare. In *Anthemis Cotula* 11 and 9 appeared as transition modes between 13 and 8; 9 also appeared momentarily in *Zinnia Haageana*, *Z. tenuiflora*, and *Laya platyglossa;* and 11 and 12 in *Sanvitalia procumbens*. In three heterocarpous species, *Dimorphotheca pluvialis*, *Laya platyglossa*, and *Sanvitalia procumbens*, the plants grown from the two kinds of seeds produced essentially like variation curves. The same thing was true of plants grown in different years and in different environments, the modal numbers and characteristic slopes of the periodicity curves remaining unchanged for the particular species, though the mean values were considerably modified.—Geo. H. Shull.

Roots of Psaronius.—Since the removal of the great mass of the marattiaceous plants of the Paleozoic to the seed plants, more critical attention has been given to *Psaronius* as the sole evidence of the existence of the Marattiaceae at that early period. Among the structures differentiating *Psaronius* from modern Marattiaceae, the most striking is the difference in the location of the secondary roots in relation to the stem. In the modern representatives of the family these roots bore their way for a considerable distance through the cortex of the stem before they penetrate to the surface. At all points in their course they are sharply marked off from the cortex by remnants of broken-down cells. In *Psaronius* they form a wide zone in the cortex of the stem in which there are no remnants of leaf traces or leaf scars, and no sharp distinction between the root cortex and the parenchyma in the interstices between the roots. Stenzel's explanation of this root layer as homologous with the outer cortex of the Marattiaceae has passed current without question until the last ten years. In 1902 Farmer and Hill suggested that the parenchyma in the interstices of the roots of *Psaronius* might be of the nature of hairy outgrowths rather than cortical parenchyma of the stem.

The question thus raised has been attacked by Solms-Laubach[19] with convincing results. He worked cheifly with thin sections of fossils (*P. Haidingeri*) from Manebach, supplemented by material from the Museum of Rio

[19] Solms-Laubach, H. Grafen zu, Der tiefschwarze *Psaronius Haidingeri* von Manebach in Thüringen. Zeitschr. Bot. **3**: 721–757. *figs* 7. 1911.

Janeiro. He finds that, unlike the modern Marattiaceae, *Psaronius* has a thin cortex bounded on the outside by a massive hypodermal sclerenchyma layer. From the outer region of this sclerenchyma layer or from the epidermis strands of tissue develop by a secondary activity of the cells, giving rise to a clothing of multicellular hairs on the surface of the stem. Where the secondary roots make their way through the cortex and sclerenchyma layer, they are limited, as in modern Marattiaceae, by a definite epidermis and by a zone of disintegrated cortical cells. But after they have penetrated the sclerenchyma layer, no such clearly marked boundary is perceptible, for here the roots pass downward among the multicellular hairs on the outside of the stem. They are consequently imbedded in the hairs which form a filling tissue between them, closely applied to the stemward sides of the roots. Then, in turn, the hypodermal layer of the cortex of the roots starts into activity. The resulting cells are few on the inner surface of the roots, where the hairs from the stem are in contact with them, while on the outwardly turned face they develop outgrowths similar to the multicellular hairs of the stem. These in turn make an imbedding layer for younger roots whose origin is higher in the stem, and which grow downward over the root surfaces as the first roots grew over the stem. While the hairs of the stem fill the crevices between the first roots and are soon overgrown by them, similar outgrowths from the roots fill the spaces between the successive layers of roots. Each system of hairs stops its growth in so short a time that a meristematic part of the tissue can never be detected. No branching of the filling tissues appears, because of the constant correspondence between the increase in the circumference of the stem and the number of cell rows in the filling tissue, due to the increase in the number of points of origin.

If it were possible to follow a root throughout its course, it would be found to be organized in three parts: a proximal part, in which it breaks its way through the cortex of the stem; a middle part, applied to the filling tissue arising from the stem; and a distal part, in which the subepidermal cortical tissue develops. The so-called "inner" and "outer" roots of *Psaronius* illustrate the two last mentioned portions.

In an attempt to find whether this peculiar development of the outer cortex is present in plants related to *Psaronius*, SOLMS-LAUBACH examined a stem of *Xylopsaronius*. Though its poor state of preservation made definite conclusions impossible, the presence of the root of another plant between the sclerenchyma layer of the stem and the inner roots is strong evidence of a resemblance. In confirmation of this, SCHÜSTER[20] has shown complete correspondence between a well-preserved root system of *Xylopsaronius* and *Psaronius*. The tissue formerly interpreted as secondary xylem in the root of *Xylopsaronius* is in reality secondary filling tissue originating from the cortex like that described in *Psaronius* by SOLMS-LAUBACH. His photomicrograph of

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[20] SCHÜSTER, J., *Xylopsaronius*, der erste Farn mit secundärem Holz? Ber. Deutsch. Bot. Gesells. **29**: 545–548. 1911.

the stem is strong evidence in support of the interpretation of the filling tissue as peculiar outgrowths. Nothing comparable to such multicellular hairs on roots has been found in present ferns, although it is possible that examination of tropical tree ferns may reveal traces of similar structures.—GRACE M. CHARLES.

The development of Pyronema confluens.—Believing that the alternation of generations has not yet been satisfactorily worked out in any fungus, CLAUSSEN[21] has completed an extensive cytological and morphological study of the development of *Pyronema confluens*, a form already investigated by HARPER[22]. The spores germinate immediately on being discharged from the ascus. He finds that under favorable conditions any cell of the fungus may develop into a complete plant. In material grown on agar at 20° C. in direct sunlight, he finds that the vegetative mycelium is produced in 1–2 days; the fruit bodies begin to form in 2–3 days; fertilization occurs in 3–4 days and the first ascogenous hyphae appear; after 5 days the recurved tips of the ascogenous hyphae are observable; young asci may be found on the sixth day, at which time 1, 2, 4, and 8-spored asci are present. In cultures under these conditions the fungus completes its development in 7–8 days. CLAUSSEN observed that the younger stages of the fruit bodies often arise from dichotomously branched aerial hyphae, so that they are often stalked. His observations as to the origin of the sexual organs agree in general with the earlier descriptions of DE BARY[23] and of KIHLMAN.[24] The hyphae, which bear the ascogones, and those which bear the antheridia, may arise from the same mycelial thread; the fungus, therefore, is homothallic.

The mycelium consists of multinucleate cells. Protoplasmic streaming was observed in the hyphae, indicating that there is a pore in the cross-walls, connecting the contents of adjacent cells. The hyphal branches which bear the sexual organs are always multinucleate. CLAUSSEN is unable to determine whether or not nuclear division occurs in the ascogone and in the antheridium before fertilization. So far as he is able to discover, the nuclei in the sexual organs are exactly alike. When the sex organs are mature, he observes that the nuclei increase in size, but that there is a more marked increase in the size of the nuclei of the ascogone. Certain nuclei in both male and female organs degenerate before the sexual act. The phenomena concerned in the fusion of the antheridium with the trichogyne, the passage of the male nuclei into the

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[21] CLAUSSEN, P., Zur Entwicklungsgeschichte der Ascomyceten. *Pyronema confluens*. Zeitschr. Bot. **4**: 1–64. *pls. 6. figs. 13.* 1912.

[22] HARPER, R. A., Sexual reproduction in *Pyronema confluens* and the morphology of the ascocarp. Ann. Botany **14**: 321–400. 1905.

[23] DE BARY, A., Ueber die Fruchtentwicklung der Ascomyceten. Leipzig. 1863.

[24] KIHLMAN, O., Zur Entwicklungsgeschichte der Ascomyceten. Acta Soc. Scient. Fenn. **13**: 29–40. 1883.

trichogyne and thence into the ascogone, is essentially as has been described by HARPER and others. After the sexual act is completed and the trichogyne is again cut off from the ascogone, many nuclei were observed in the ascogone in pairs. On account of the slight difference in size of the paired nuclei and of the nucleoli, he believes each pair consists of a male and female nucleus. A fusion of these paired nuclei does not occur in the ascogone, but they enter the ascogonous hyphae in pairs. BROWN[25] holds that there is no fusion of the sexual nuclei in the ascogonium. He holds that an appearance quite like fusion results from division of the nuclei, the daughter nuclei remaining closely associated.

The ascogenous hyphae were observed to develop in several different ways. Whatever the method of their development, CLAUSSEN believes that the sexual nuclei and their progeny formed by conjugate division remain entirely distinct. A pair of each of the nuclei finally enters the young ascus, where they fuse to form the primary ascus nucleus. CLAUSSEN finds it difficult to make out the structure of the fusion nucleus of the ascus. He is convinced that the first division of this nucleus is heterotypic, and finds a synaptic contraction and a diakinesis, in which there are about 12 bivalent chromosomes. At no point in nuclear division has he been able to distinguish central bodies with certainty. In the second and third divisions of the ascus nuclei he fails to find a synaptic contraction or a diakinesis stage. The number of chromosomes in these divisions is about twelve. The process of spore formation and spore delimitation is essentially as described by HARPER.

According to CLAUSSEN, the spore, mycelium, and sexual organs constitute the gametophyte, while the ascogenous hyphae represent a sporophyte not sharply separated from the gametophyte. The ascus is a spore mother cell. The sporophyte, instead of having nuclei with double chromosome numbers, contains male and female nuclei in pairs, which divide by conjugate division. The nuclear divisions in the ascus, except the first, have no significance in the alternation of generations in this fungus.—J. B. OVERTON.

Cytology of Laboulbeniales.—In a short introductory account based on the results of his studies of the cytology of a number of forms of the Laboulbeniales, FAUL[26] gives the general outlines of the morphology of this group. The spores in the earliest stages of their formation are uninucleate, but before the spore is mature the nucleus divides and a septum is formed, dividing the spore into two cells. In *Amorphomyces* alone the septum is not formed and the nucleus degenerates. The cells of the thallus are characteristically uninucleate, but after the thallus has completed its growth some of the

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[25] BROWN, W. H., Nuclear phenomena in *Pyronema confluens*. Johns Hopkins Univ. Circ. **6**:42–45. 1909.

[26] FAUL, J. H., The cytology of the Laboulbeniales. Ann. Botany **25**:649–654. 1911.

larger cells become multinucleate. The nuclear divisions are mitotic throughout. The antheridia in all cases are uninucleate. In the forms with exogenous antheridia the uninucleate spermatia arise as branchlike outgrowths from the antheridia. It is probable that the antheridial nucleus divides repeatedly to furnish nuclei for the successively formed spermatia. In the forms with endogenous antheridia, the antheridial nucleus divides and the sperm nucleus is pushed out by the spindle fibers toward the opening of the antheridium through which the spermatia are discharged. The spermatia consist of the relatively large nucleus, apparently surrounded by only a little cytoplasm, and the protoplasmic membrane. The antheridial nucleus divides repeatedly to form successive sperm nuclei which are ejected by the spindle fibers in the peculiar manner described.

The origin of the binucleate state of the carpogenic cell was made out only in *Laboulbenia chaetophora*, which has no antheridia. In the other forms neither the entrance of the sperm nucleus into the trichogyne nor its migration through the trichophoric cell has been observed. In *Laboulbenia chaetophora* the nuclei of the trichophoric and the carpogenic cells divide, and one nucleus from each pair ultimately constitutes a member of the pair in the carpogenic cell. From the carpogenic cell the ascogonium and ascogenous cells are formed after a series of conjugate nuclear divisions. Asci bud off directly from the binucleate ascogenous cells. The subsequent processes of nuclear fusion in the ascus and spore formation differ in no essential detail from the analogous processes among the Ascomycetes with which the Laboulbeniales are usually classed.

The conclusion drawn by the author from the cytological study of the Laboulbeniales is that they belong to the Ascomycetes, and more particularly, on account of the possession of a perithecium, to the Pyrenomycetes. The phenomena occurring in the ascus appear to lend some support to this classification, but the author's attempt to homologize the perithecium of the Laboulbeniales with that of the Pyrenomycetes would seem to need further support. Thus far the unique development of the perithecium of the Laboulbeniales has no known analogies among the Ascomycetes.—H. HASSELBRING.

Sexuality in mosses.—MARCHAL,[27] in a study of sexuality in mosses, makes a comparison of a dioicous species, *Bryum caespiticium*, with a number of synoicous species, chief among which is *Amblystegium serpens*. In the dioicous species one-half of the spores give rise to protonemata which produce antheridial plants, the other half produce archegonial plants. Fertilization produces a bisexual sporophyte and the sex characters are separated in the reduction division. Consequently two members of the tetrad are always male and two female, as has actually been shown in *Sphaerocarpus*. In synoicous forms the

[27] MARCHAL, EL., La sexualité chez les Mousses. Bull. Soc. Roy. Belgique **47**: 277–285. 1911.

gametophores from protonemata produced by spores, as well as those from secondary protonemata rising from the stem, leaves, and even from the wall cells of antheridia and archegonia, are always bisexual, and the sex characters are not separated until the last division of the spermatogenous and the oogenous cells. The sex characters are united by fertilization and not separated in the tetrad. Therefore in dioicous mosses the sex characters are separate in the spores, protonemata, gametophores, sperms, and eggs, but not in the sporophyte; in synoicous mosses the sex characters are separate only in the egg and sperm.

MARCHAL is able to induce apospory in the capsule of *Bryum caespiticium*. Gametophores rising from an aposporous protonema are *always synoicous*, but the eggs are never fertilized. He concludes that dioicous mosses which have become synoicous through apospory are irremediably sterile. In the synoicous *Amblystegium serpens* apospory was also induced, and the resulting gametophores produced eggs capable of being fertilized. In the $4x$ sporophytes from these fertilized eggs, apospory was again induced, but the $4x$ leafy shoots, although exceptionally vigorous, have as yet remained persistently sterile. The same results were obtained in other synoicous species, *Amblystegium subtile*, *Barbula muralis*, and many others which the author does not name. He states that *Ephemerum serratum* and *Funaria hygrometrica* are synoicous. Miss SPEER, working in the Hull Botanical Laboratory, first showed that the latter species is occasionally synoicous. MARCHAL is at present studying a sterile synoicous *Bryum atropurpureum* which he believes is a natural aposporous derivative of the common dioicous form.

There are no illustrations, and no definite information as to how the presence of $2x$ and $4x$ numbers in the aposporous derivatives were proved; nor are the methods for inducing apospory and for continuing the cultures given in detail. It is an admirable piece of much-needed research, but the lack of a definite and detailed statement of methods is a very unfortunate omission, since many investigators look with suspicion on the work of those who are secretive as to methods when fundamental problems are concerned.—W. J. G. LAND.

Phytomyxaceae.—SCHWARTZ, who has recently made several contributions to our knowledge of the parasitic slime molds, gives an account[28] of another form which he found on the roots of *Poa annua* and other grasses. The organism, to which he gives the name *Sorosphaera graminis* without, however, adding a formal diagnosis, is closely related to *S. Junci*, which the author discovered in the roots of sedges. The organism was found most abundant on plants whose roots were hypertrophied by eelworms. It is not usually found, however, in the swollen parts, nor does the organism itself produce any form of hypertrophy. The life-history of *S. graminis* does not

[28] SCHWARTZ, E. J., The life-history and cytology of *Sorophaera graminis*. Ann. Botany **25**:792–797. 1911.

differ from that of *S. Junci*, but some of the stages appear to be more easily observable in *S. graminis*. The youngest stages are uninucleate amebae. These fuse to form plasmodia which grow until they occupy the entire host cell. The nuclei of the growing plasmodia all divide repeatedly and simultaneously in the manner described for other members of the Plasmodiophoraceae. At the close of the vegetative stage the akaryote or chromidial stage begins. The nuclei lose their contents, leaving only vacuoles in their place. Within these vacuoles apparently fresh nuclei are organized. These undergo mitotic divisions, after which the plasmodium is broken up by cleavage into small uninucleate masses which become the spores. Under the classification of MAIRE and TISON, this form would be placed in their genus *Ligniera*, which includes those species of the Plasmodiophoraceae which lack the schizogenous stage and do not cause swelling on their host plants.—H. HASSELBRING.

Zygopteris.—SCOTT[29] has studied sections of a new specimen of *Zygopteris Grayi*, and finds that it is an *Ankyropteris*, as BERTRAND had pointed out, on the basis of the presence of peripheral loops on the leaf trace. The vascular cylinder of the stem (a 5-rayed star in section) is regarded as "a highly elaborated protostele," there being at present no evidence for the existence of a true pith in any member of the group. This is certainly a simpler interpretation of the pithlike region with interspersed tracheids than to regard the cylinder as a "condensed" polystelic structure. It would be even simpler to eliminate "highly elaborated," and to call the cylinder an incomplete protostele. The problematical and abundant "aphlebiae" are found to be "modified basal pinnae of the leaf, as shown by the structure and mode of origin of their vascular strand."—J. M. C.

Effect of temperature on respiration.—KUIJPER,[30] while at the Buitenzorg laboratories, determined the CO_2 production by seedlings of *Arachis hypogaea* and *Oryza sativa* at various temperatures from 15° C. to 50° C. He finds that the effect of temperature on respiration of the tropical plants studied is the same as on plants in the temperate zone.[31] But the "critical temperature" (temperature at which a high respiratory intensity is maintained for a considerable time) of *Arachis hypogaea* is 5°–10° higher than that previously found for *Pisum* and *Lupinus*. KUIJPER thinks this difference is due to their surroundings. The mean temperature at Java is about 10° higher than the mean temperature of the vegetation period of the temperate zone.—SOPHIA H. ECKERSON.

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[29] SCOTT, D. H., On a paleozoic fern, the *Zygopteris Grayi* of Williamson. Ann. Botany **26:** 39–69. *pls. 1–5. fig. 1.* 1912.

[30] KUIJPER, J., Einige weiteren Versuche über den Einfluss der Temperatur auf die Atmung der höheren Pflanzen. Ann. Jard. Bot. Buitenzorg II. **9:** 45–54. *pls. 6, 7.* 1911.

[31] BOT. GAZ. **50:** 233. 1910.

Doubling of embryo sac.—COMPTON[32] reports an interesting situation in a *Lychnis* hybrid, in which an ovule contained two embryo sacs, each penetrated by a pollen tube, and each containing a two-celled embryo. He calls this "a curious example of duplicity." The closing statement is worth remembering: "The fact that two pollen tubes should enter and fertilize an ovule which had developed two embryo sacs can hardly be a mere coincidence; rather it would seem to indicate a quantitative relation between embryo sac and pollen tube in the matter of chemotaxis, two embryo sacs excreting sufficient of the chemotropic substance to attract two pollen tubes."—J. M. C.

Seedling structure of Centrospermae.—HILL and DEFRAINE[33] have recorded the results of an extended survey of the transition phenomena of the seedlings of Centrospermae. The "theoretical considerations" are to be presented later, but in the present paper there are indications of what they may be. The families presented, through abundant representatives, are Portulacaceae, Caryophyllaceae, Amarantaceae, Chenopodiaceae, Phytolaccaceae, Aizoaceae, and Nyctaginaceae. The authors state that "no very striking results" were obtained, and that the chief interest is connected with the features of the last-named family.—J. M. C.

Fall of leaves.—Based upon a mass of data collected largely from the literature, COMBES[34] shows that the conception of SACHS regarding the migration of substances at the time of leaf fall is no longer tenable. The substances that do not disappear from the leaves, as well as those that accumulate in them before their fall in the autumn, are not to be considered a priori as substances non-utilizable or toxic for the plant containing them. The fallen leaves contain an important percentage of substances that would have been utilizable by the plant.—CHAS. O. APPLEMAN.

Morphology of Viola.—Miss BLISS[35] has studied five species of *Viola* with reference to the structures connected with the embryo sac. The hypodermal archesporial cell, the tapetal cell, the linear tetrad, and all the antefertilization structures of the sac are what may be regarded as normal for angiosperms. Double fertilization was observed in *V. cucullata*. "There is no suggestion of a suspensor," and the embryo, surrounded by a solid mass of endosperm, is bright green.—J. M. C.

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[32] COMPTON, R. H., Note on a case of doubling of embryo sac, pollen tube, and embryo. Ann. Botany **26**: 243, 244. 1912.

[33] HILL, T. G., and DEFRAINE, ETHEL. On the seedling structure of certain Centrospermae. Ann. Botany **26**: 175–199. *figs. 15*. 1912.

[34] COMBES, RAOUT, Les opinions actuelles sur les phenomènes physiologiques qui accompagnent la chute des feuilles. Rev. Gén. Bot. **23**: 129–264. 1911.

[35] BLISS, MARY C., A contribution to the life history of *Viola*. Ann. Botany **26**: 155–163. *pls. 17–19*. 1912.

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SPERMATOGENESIS IN EQUISETUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 158

LESTER W. SHARP

(WITH PLATES VII AND VIII)

Historical résumé

The cilia-bearing organs of the motile cells of plants have formed the basis of a number of researches during recent years. In the majority of cases in which the bearing of the results has been given consideration, the discussion has centered about the morphological nature of these organs, and in this discussion a very prominent place has been taken by the centrosome.

Among the earliest investigations in this field were those of STRASBURGER (**78**) on the algae. During the development of the swarm spores of *Oedogonium*, *Cladophora*, and *Vaucheria* he found that the nucleus approaches the plasma membrane, which at that point becomes thickened, forming a lens-shaped *Mundstelle*. From this grow out the cilia, and at the base of each a small refractive granule is present. A full discussion of the morphological nature of these cilia-bearing structures and an extensive comparison with those of higher plants were given in connection with a later work (**80**). The main point to be noted at this time is that STRASBURGER believed that the blepharoplasts of higher plants have been derived from such swollen *Hautschicht* organs in the algae, and that all of them are morphologically distinct from centrosomes.

DANGEARD (**17**) found a deeply staining granule at the base of the cilia in *Chlorogonium*, but did not consider it a centrosome. In

a later paper (**18**) he states that in *Polytoma* the cilia are inserted on a similar granule which is believed to be a swelling of the ectoplasm. In some cases he saw a delicate filament connecting this with another minute body at the surface of the nucleus.

In *Hydrodictyon* (TIMBERLAKE **85**) the cilia are inserted on a small body lying in contact with the plasma membrane, but independent of the latter. Protoplasmic strands join this structure with the nucleus. At the poles of the spindle during the differentiation of the spore *Anlage*, and later near the nucleus, two heavily staining granules were seen, but their origin and further history were not worked out.

In the zoospore origin of *Derbesia*, according to DAVIS (**21**), the nucleus migrates toward the cell membrane and from it many granules, which are not centrosomes, move out along radiating strands of cytoplasm to the surface of the cell, where by fusion they form a ring-shaped structure from which the cilia develop.

The development of the spermatozoid in *Chara* has been described by BELAJEFF (**2**) and by MOTTIER (**71**). Here the blepharoplast arises as a differentiation of the plasma membrane and bears two cilia. No centrosomes or *Plasmahöcker* were observed at the base of the cilia, although SCHOTTLÄNDER (**75**) had previously reported centrosomes in the cells of the spermatogenous filament.

GRIGGS (**34**) describes in a recent paper a deeply staining body at the insertion point of the cilia in the zoospore of the fungus *Rhodochytrium*. This is connected by fine cytoplasmic fibers with the nucleus. The author states that no centrosomes were observed.

In the myxomycete *Stemonitis* JAHN (**56**) has made a highly suggestive observation. During the last mitosis in the formation of the swarmers the spindle poles are occupied by centrosomes. During the anaphases the flagella of the two resulting swarmers are seen growing out directly from these centrosomes.

Among the bryophytes the blepharoplasts in *Marchantia* and *Fegatella* have received the most attention. According to IKENO (**53**) a centrosome comes out of the nucleus at each spermatogenous division in *Marchantia* and divides to two, which diverge to opposite

sides of the cell, occupy the spindle poles, and disappear at the close of mitosis. It is possible that they are included within the membranes of the daughter nuclei. After the last (diagonal) division, however, they remain in the cytoplasm as the blepharoplasts, elongating and bearing two cilia. IKENO regards these bodies as true centrosomes. He further believes that the blepharoplasts of pteridophytes and gymnosperms are derived ontogenetically or phylogenetically from centrosomes, but that all bodies called centrosomes in plants may not be homologous. In a paper appearing two years later, MIYAKE (**66**) states that although an inconstant aster, often with a dot at the focus, may appear in the spermatogenous divisions, no body like IKENO'S centrosome is present, except at the last mitosis, when a body lies at each spindle pole as figured by that author. Essentially the same results were obtained in *Fegatella*, *Pellia*, *Aneura*, and *Makinoa*. MIYAKE believes that the centrosome hitherto reported in the cells of the Hepaticae is nothing but a center of cytoplasmic radiation, and inclines toward the view of STRASBURGER that the blepharoplast and the centrosome are not homologous structures. ESCOYEZ (**22**) states that in *Marchantia* and *Fegatella* two "corpuscles" appear in the spermatid mother cell in contact with the plasma membrane. These occupy the spindle poles and in the spermatids function as blepharoplasts. ESCOYEZ regards these organs as distinct from centrosomes, though their origin was not traced. Centrosomes are reported by SCHAFFNER (**74**) in all the spermatogenous divisions in *Marchantia*. After the last mitosis these behave as blepharoplasts, which are consequently looked upon as modified centrosomes. BOLLETER (**8**) found in *Fegatella* a centrosome-like body near the spindle pole at the last division and observed its nuclear origin. He believes that it is present in the earlier division also.

In the antheridium of *Riccia* LEWIS (**61**) reports centrosome-like structures in the early and diagonal divisions. These apparently arise *de novo* in the cytoplasm at each mitosis, showing no continuity through the succeeding cell generations except at the last mitosis, when they persist and become the blepharoplasts. LEWIS does not think these bodies represent centrosomes.

The most recent investigations of the blepharoplast in bryo-

phytes are embodied in two papers appearing in 1911. In the first of these WOODBURN (**95**) gives an account of spermatogenesis in *Porella*, *Asterella*, *Marchantia*, and *Fegatella*. He finds that the blepharoplast is first distinguishable as a spherical granule in the cytoplasm of the spermatid, and holds that it represents, as MOTTIER (**71**) had formerly suggested, an individualized part of the kinoplasm arising *de novo* in certain spermatogenous cells. WILSON (**93**) describes the phenomena occurring in *Pellia*, *Atrichum*, and *Mnium*. In *Mnium* and *Atrichum* the spermatogenous divisions show no centrosomes, while in *Pellia* centrospheres, and probably centrosomes, are present during the later mitoses. The origin of the blepharoplast as here described is very peculiar. In the spermatid of *Mnium* a number of bodies separate from the nucleolus and pass out into the cytoplasm where they coalesce to form a "limosphere." The nucleolus then divides into two masses, both of which pass into the cytoplasm; one functions as the blepharoplast while the other gives rise to an accessory body. In *Atrichum* the first body separated from the nucleolus becomes the blepharoplast, a second forms the limosphere, and a third the accessory body. In *Pellia* the origin of these structures was not determined. In all three plants the blepharoplast goes to the periphery of the cell and produces a threadlike structure along the plasma membrane. The nucleus then moves against this thread and the two metamorphose together to form the spermatozoid. WILSON regards the blepharoplast as "probably derived from a centrosome."

According to HUMPHREY (**49**) the blepharoplast of *Fossombronia* is first seen in the cytoplasm of the spermatid.

The early papers dealing with the spermatozoid in pteridophytes, such as those of BUCHTIEN (**9**), CAMPBELL (**12**), BELAJEFF (**1**), GUIGNARD (**35**), and SCHOTTLÄNDER (**75**), give us little or no information concerning the development of the blepharoplast. Our more definite knowledge of this subject dates from 1897, when BELAJEFF published three short papers. In the first of these (**3**) it is stated that the fern spermatozoid consists of a thread-shaped nucleus and a plasma band, with a great many cilia growing out from the latter. In the plasma band is inclosed a thin thread which arises by the lengthening of a small body seen in the sperma-

togenous cell. In the second paper (**4**) the blepharoplast of *Equisetum* is first described as a crescent-shaped body lying against the nucleus of the spermatid. This body stretches out to form the cilia-bearing thread. The third contribution (**5**) is a short account of the metamorphosis of the spermatid in *Chara*, ferns, and *Equisetum*. In all of these forms a small body elongates to form a thread upon which small *Höcker* arise and grow out into cilia. In a comparison with animal spermatogenesis, BELAJEFF here homologizes the *Körperchen* (blepharoplast) in the spermatid, the thread to which it elongates, and the cilia of the plant, with the centrosome, middle piece, and tail (perhaps only the axial filament), respectively, of the animal. The following year, in connection with a further discussion, he figured the details as made out by him in *Gymnogramme* and *Equisetum* (**6**). In *Gymnogramme* the blepharoplasts appear at opposite sides of the nucleus in the spermatid mother cell, while in *Equisetum* a single blepharoplast is first figured lying close to the nucleus of the spermatid, behaving as outlined in the earlier accounts.

One of the most interesting cases is that of *Marsilia*, first described by SHAW (**76**). According to this investigator a small granule or "blepharoplastoid" appears near each daughter nucleus of the mitosis which differentiates the grandmother cell of the spermatid. During the next division these divide but soon disappear, and a blepharoplast appears near each spindle pole. In the next cell generation (spermatid mother cell) the blepharoplast divides to two which become situated at the spindle poles in the final mitosis. In the spermatid the blepharoplast shows a small internal granule; this multiplies to several and forms a band which elongates spirally with the nucleus and bears the cilia. SHAW sees in these facts no ground for the homology of the blepharoplast and the centrosome. BELAJEFF'S paper dealing with *Marsilia* appeared in the following year (**7**). He found that centrosomes occur at the poles during all, excepting possibly the first, of the series of divisions which result finally in the 16 spermatids. After each mitosis the centrosome divides to two which occupy the poles during the next mitosis, and in the spermatid it performs the function of a blepharoplast. BELAJEFF regards this as a strong confirmation

of his theory that the blepharoplast and the centrosome are homologous structures.

In *Adiantum* and *Aspidium* (THOM **84**) the blepharoplast is described as a round body in the cytoplasm of the spermatid. It is stated that it does not act as a centrosome during division, though no figures of these stages are shown.

The most recent work dealing with the blepharoplast in pteridophytes is that of YAMANOUCHI (**97**) on *Nephrodium*. In this form there are no centrosomes in the whole life history. The two blepharoplasts, which arise *de novo* in the cytoplasm of the spermatid mother cell, take no active part in nuclear division, merely lying near the poles of the spindle. In the spermatid the blepharoplast elongates in close union with the nucleus to form the cilia-bearing band.

The first known blepharoplast in plants above the algae was discovered in *Ginkgo* by HIRASÉ (**45**) in 1894. He observed two, one on either side of the body cell nucleus, and because of their great similarity to certain structures in animal cells believed them to be attraction spheres. It was not until two years later that this investigator announced the discovery of the swimming sperm of *Ginkgo*. In 1897 WEBBER (**89**) observed the same structures, noting their cytoplasmic origin. On account of several differences existing between these bodies and known centrosomes he expressed the belief that they are not true centrosomes, but distinct organs of spermatic cells, and first applied to them the name blepharoplast. FUJII (**30, 31, 32**) gave several figures of spermatogenesis in *Ginkgo*, which agree with the accounts of HIRASÉ and WEBBER. The same subject has been dealt with more recently by MIYAKE (**67**).

In two short papers appearing in 1897, WEBBER described the blepharoplast of *Zamia* (**87, 88**), and in 1901 a very full account was published (**90**). According to this author two blepharoplasts arise *de novo* in the cytoplasm. They are surrounded by radiations up to the time of the division of the body cell, but these have no part in the formation of the spindle, which is entirely intranuclear. During mitosis the blepharoplasts, lying opposite the poles, become vacuolate and break up to many granules which unite to form the

cilia-bearing band. In this paper WEBBER gives a very extensive discussion of the morphological nature of the blepharoplast which will be referred to later.

IKENO (**51**) expressed the opinion that the blepharoplast of *Ginkgo* and the cycads is not only similar to a centrosome but is a true centrosome, a view shared by GUIGNARD (**36**). Soon after this IKENO's full account of gametogenesis and fertilization in *Cycas* appeared (**52**). In this paper it was shown that the blepharoplasts appear in the body cell, lie opposite the spindle poles during mitosis, and break up to granules which fuse to form the spiral band in a manner similar to that described by WEBBER for *Zamia*.

Several years later the same writer published two papers dealing with the morphological nature of the blepharoplast. In the first of these (**54**) he reviews the former work on the subject and makes comparisons with analogous phenomena in animals, which he believes sustain the homologies of BELAJEFF. He points out that in *Marchantia* centrosomes are present in all the spermatogenous divisions, while in other liverworts they appear much later, and from this argues that the bryophytes show various stages in the elimination of the centrosome. He strongly reasserts his belief that blepharoplasts are centrosomes and speaks of the "Umwandlung eines Zentrosoms zu einem Blepharoplast" in the development of a spermatid into a spermatozoid. The *Hautschicht* organs of the algae are also held to be ontogenetically or phylogenetically derived from centrosomes. In the later contribution (**55**) he insists less strongly upon the morphological identity of all blepharoplasts, separating them into three categories: (1) centrosomatic blepharoplasts, including those of the myxomycetes, bryophytes, pteridophytes, and gymnosperms; (2) plasmodermal blepharoplasts, those of *Chara* and some Chlorophyceae; (3) nuclear blepharoplasts, found only in a few flagellates.

The blepharoplasts of *Microcycas* (CALDWELL **11**) appear in the cytoplasm of the body cell, often very close to each other. They are surrounded by prominent radiations and lie opposite the spindle poles through mitosis. At metaphase they have already broken up and begun the formation of the spiral band.

CHAMBERLAIN (**15**) observed in the cytoplasm of the body cell

of *Dioon* a number of very minute "black granules" which he was inclined to believe originate within the nucleus. Very soon two undoubted blepharoplasts are present, and are apparently formed by the enlargement of two of the original black granules. Very conspicuous radiations develop about them, and after mitosis they form the cilia-bearing band as in other cycads. In an earlier paper (13) on the homology of the blepharoplast CHAMBERLAIN expressed the opinion that it is to be regarded as a centrosome.

From the foregoing historical review it is evident that there are two general views concerning the morphological nature of the blepharoplast as seen in bryophytes, pteridophytes, and gymnosperms:

(1) The blepharoplast represents a centrosome (HIRASÉ, IKENO, BELAJEFF, GUIGNARD, SCHAFFNER, WILSON, CHAMBERLAIN).

(2) The blepharoplast is specialized kinoplasmic or cytoplasmic material but not a centrosome (STRASBURGER, WEBBER, SHAW, LEWIS, THOM, ESCOYEZ, WOODBURN).

The present study of spermatogenesis in *Equisetum* was undertaken in the hope of shedding further light upon the relative merits of these two views, and it is with particular reference to this problem that the results are given consideration in the following pages.

Materials and methods

Spores were collected in Chicago, May 15, 1911, and sown upon clean sand watered from below. These cultures were kept under ground glass in the greenhouse of the Hull Botanical Laboratory. In five weeks, a somewhat longer time than is usually necessary, sperms were swimming in large numbers.

Several killing fluids and stains were used. By far the most satisfactory results were obtained with the iron-hematoxylin of Haidenhain after a killing fluid made up as follows: bichromate of potash 2.5 gm., bichloride of mercury 5 gm., water 90 cc., freshly distilled neutral formalin 10 cc.

Description

The usual statement concerning the antheridium of *Equisetum* is that it occurs in two forms, developing in some cases like the antheridium of the eusporangiate pteridophytes, and in others from a

papillate cell as in the Filicales. The mode of development has usually been correlated with the position of the antheridium initial in the prothallium. An adequate study of antheridium development was not made in connection with the present work on *Equisetum arvense*, but of the many young antheridia examined not one was unmistakably of the latter form. Apparently any of the cells of the prothallium, especially those near the apex, are able to divide periclinally and produce antheridia of the well known imbedded type.

In the nuclei of the spermatogenous cells the chromatin has the form of a ragged network of rather close mesh, the greater part of it being accumulated in knots at the intersections. One or more conspicuous nucleoli are present. The cytoplasm during the earlier cell generations may contain many plastids in various stages of disorganization; in most cases these are no longer evident by the time the 8 or 16-celled stage has been reached, but occasionally they persist and are found in considerable numbers in the penultimate cell generation, or even in the spermatids. It is obviously necessary to select for critical study of the details of blepharoplast development those antheridia in which the plastids do not introduce an element of uncertainty.

The main point to be noted in connection with mitosis in the early cell generations is that there are present no bodies which could possibly be interpreted as centrosomes. The spindle fibers are very weakly developed and end at the poles without any signs of centrosomes, centrospheres, or asters.

The first conspicuous indication of approaching sperm formation is seen in the rounding off of the cells of the penultimate generation (fig. 1). They begin to separate at the corners and gradually draw away from each other until they are entirely free. Although the division of these cells results in the production of sperms n pairs, it becomes inaccurate to speak here of mother cells with two sperms developing in each, since the intervening walls may persist until the sperms are mature or may break down at once. By designating them "penultimate cells" this ambiguity is avoided. Their number at the time of rounding off varies greatly in different antheridia. The observed range was 64 to 512, which means that

the number of sperms per antheridium varies from 128 to 1024 (approximately). Correlated with this is a great difference in the size of the antheridia. The sperms themselves also show considerable variation in dimension, as a comparison of figs. 28 and 29 will show. The nucleus of the penultimate cell at the time of separation is in the resting condition. The cytoplasm has a very fine and uniform structure, and in most cases is entirely free from plastids or other inclusions. Vacuoles are present only very rarely.

While the penultimate cells are rounding off from one another there appears in the cytoplasm near the nucleus a very minute granule which stains intensely with iron-hematoxylin (fig. 2). Its diameter lies between 0.25 and 0.3 μ. Very faint cytoplasmic radiations extend out from it in all directions, forming a very weakly developed aster. In other cells of the same antheridium the granule is seen to be dumb-bell shaped, and in still other cells distinctly double, showing that it divides to two (figs. 3, 4). These paired bodies are the blepharoplasts. Immediately after division their diameter increases to 0.5 μ. Their radiations become more pronounced and the nucleus often becomes flattened or slightly indented at the point where they lie, as in fig. 8.

The origin of the single granule cannot be stated with certainty. When first made out it holds a position near the nuclear membrane, a fact which would suggest its nuclear origin, but no other evidence in favor of this interpretation was obtained. The nuclear membrane shows no indication of recent disturbance. Moreover, it is highly improbable that such a granule could be distinguished within the nucleus because of its small size, its similarity in staining reaction to the chromatin network, and the density of the latter. Some light may be shed upon the question by exceptional cells like that shown in fig. 5. Here are scattered through the cytoplasm many very small intensely staining bodies, a few of which occur in pairs. When first seen these granules lie in all positions with respect to the nucleus and the plasma membrane. Some of the paired granules are distinctly larger than the single ones; the pair nearest the nuclear membrane is always the largest, has the most evident radiations, and is without doubt the same structure shown in fig. 4.

In other cells of the same antheridium only this pair is present, the other bodies, if formerly present, having been resorbed.

One can hardly speak conclusively regarding all points in the history of such minute structures. The evidence at hand, however, inclines the present writer toward the belief that the original single granule, which by division gives rise to the two blepharoplasts, is in some cases one of a number which may appear *de novo* in the cytoplasm and start development.

The two blepharoplasts, which lie very close together for a little time immediately following their formation from a single body, soon begin to move apart. As they do so a very distinct central spindle develops between them, so that a faint but undoubted amphiaster is formed (figs. 6, 7). In some preparations the rays on the side toward the nucleus are somewhat heavier than the others and form a distinct cone (fig. 6). This feature is not made out in all cases. A line joining the two blepharoplasts may lie in any position with respect to the nuclear membrane, though the situation shown in fig. 6 is the most usual one. The blepharoplasts continue to separate, moving in paths close to the nuclear membrane, until they lie 180° apart (figs. 8–12). During the earlier stages of the migration the central spindle gradually fades out (fig. 8). The astral radiations persist, and when the blepharoplasts reach polar positions those on the side toward the nucleus become more distinct, being especially conspicuous when the blepharoplasts move a little distance away from the nucleus (fig. 13). They form two cones with the blepharoplasts at their apices, while the radiations extending in other directions remain very faint. The rays of the cone do not diverge from a single point on the blepharoplast, but pass out from a large portion of its surface. At this stage the blepharoplast may reach a diameter of 0.75 μ.

In the nucleus are now seen indications of the approaching mitosis which is to differentiate the spermatids. The nuclear reticulum gradually becomes coarser and eventually resolves itself into a spirem (fig. 14). While the spirem is segmenting to form the chromosomes the nuclear membrane breaks down and the fibers radiating from the blepharoplasts extend into the nuclear cavity and establish the karyokinetic figure. The spindle is extremely

weak in development, so that the relation it bears to the blepharoplasts is not always easily determined at this time. There is no question, however, that the blepharoplasts continue to occupy the poles (fig. 15), as would be expected after the situation in the immediately preceding stages. In the later stages of division many extremely fine strands are present between the daughter nuclei. Whether these are the remains of fibers passing from one blepharoplast to the other or represent the visible effect of the separation of the chromatin upon the cytoplasm was not determined. The cell plate separating the paired spermatids is very late in forming.

During the anaphases of karyokinesis a peculiar change occurs in the blepharoplasts. For a time they lose their affinity for iron-hematoxylin, so that in many preparations treated in the usual way with this stain they may be wholly indiscernable. In more deeply stained cells they appear as translucent bodies considerably larger than during the earlier phases of division (fig. 16). They are no longer solid but contain one or two large vacuoles, which give them in section the appearance of small rings. It is probable that the decrease in staining capacity is due to swelling through the absorption of water without any increase in stainable material. This condition exists only through the remainder of the division; when the sister spermatids are well rounded away from each other the blepharoplasts as a general rule stain deeply again. The vacuole or vacuoles form an irregular cavity, and the whole structure soon takes the form of an uneven ring (figs. 17, 18).

The blepharoplast now breaks up to several pieces which become arranged in a row, usually at once (fig. 19). These pieces multiply rapidly by further fragmentation and form a beaded chain extending about halfway around the nucleus (fig. 21). Fig. 20 shows a mass of these granules just beginning to draw out into a row.

It is at this beaded stage that the cilia begin to develop. From the blepharoplast granules there are seen very fine strands extending toward the periphery of the cell (fig. 21). Whether more than one of the strands, or rudimentary cilia, ever grow out from a single granule was not definitely determined, but since the cilia of the mature spermatozoid and the granules are approximately equivalent in number, it is probable that as a rule each granule gives rise

to one cilium. The further details of cilium development were not worked out.

The blepharoplast granules, which have been lying close together or in contact, now fuse to form a continuous thread. The coalescence usually begins at one end of the chain so that at certain stages it appears solid at one extremity and broken at the other (fig. 22). The union, although intimate, is not so complete that the thread is uniform in diameter throughout, even in the later stages. When the metamorphosis of the spermatid is half complete the beaded nature of the blepharoplast is clearly evident, and when the spermatozoids are mature it still shows an uneven outline.

Immediately after the union of the granules the nucleus begins to show marked changes. It moves to one side of the cell and begins to draw out into a flattened point next to the blepharoplast (fig. 23). At this stage the nucleus and the blepharoplast lie rather close together; the relative position of the two is seen in fig. 24, which represents a portion of a similar cell viewed from the direction *a*. The nucleus continues to elongate and quickly assumes a crescentic form, while its reticulum becomes very coarse and deeply staining (fig. 25). The blepharoplast also lengthens spirally, and the two become widely separated from one another. Figs. 26 and 27 represent respectively an entire cell like that of fig. 25 viewed from the direction *a*, and a section in the plane *ab*. No connections other than the undifferentiated cytoplasm are present between the nucleus and the blepharoplast. The cilia have now increased markedly in length.

As previously noted, the mature spermatozoids vary greatly in size in different antheridia, which may be seen by comparing figs. 28 and 29. The nucleus now stains intensely with iron-hematoxylin. Its surface presents a mottled appearance while very lightly stained sections show that its interior is quite homogeneous, with several very small vacuoles along the central region. Scattered over the nucleus, mostly along its concave face and occasionally elsewhere in the cytoplasm, are many black globules whose origin and nature were not determined. A few vacuoles are present in the cytoplasm. The blepharoplast continues its spiral growth until it has made about 1.4 turns. The nucleus makes 0.7 of a

turn, but lies parallel to the blepharoplast for 0.44 of a turn, so that the entire spermatozoid makes 1.66 turns. In all of the spermatozoids examined the direction of coiling is the same—from right to left beginning at the innermost end of the blepharoplast when the side of the cell containing the latter is turned toward the observer.

After escape from the antheridium the larger or posterior portion of the nucleus becomes extended and somewhat flattened. Both nucleus and cytoplasm absorb water and show decided enlargement, the cytoplasm, especially in the posterior portion of the spermatozoid, becoming very coarse and foamy through the great enlargement of the vacuoles. Such a mature spermatozoid fixed in the swimming condition over osmic fumes is represented in fig. 30. Exclusive of the cilia it has a length of 19.7 μ.

Discussion

The morphological nature of the blepharoplast is a topic which has been so extensively discussed by STRASBURGER, WEBBER, IKENO, and others that the present writer does not take up the subject with reference to the additional evidence afforded by *Equisetum* without risk, or even necessity, of a certain amount of repetition. In the foregoing historical résumé it was seen that the central point of the discussion has been the question of the possible morphological identity of the centrosome and the blepharoplast. Any analysis of the relationship existing between these two structures must include a consideration of the centrosome as found elsewhere in the plant kingdom, and since it has to do with a cell problem of general interest it should proceed in the light of certain phenomena occurring in the spermatogenesis in animals.

One of the earliest known centrosomes in plants was that discovered by BÜTSCHLI (**10**) in the diatom *Surirella*. It had earlier been seen by SMITH (**77**), who, however, did not recognize its true nature and termed it the "germinal dot." A full account of this centrosome was given by LAUTERBORN (**59**) in his magnificent work on the diatoms, and later by KARSTEN (**57**). It lies near the nucleus, becomes surrounded by radiations, divides and forms the central spindle of the karyokinetic figure in a very peculiar manner.

During karyokinesis it lies near the pole of the broad-poled spindle.

Centrosomes in the Sphacelariaceae have been described by STRASBURGER (**78**), HUMPHREY (**48**), and SWINGLE (**83**). In the vegetative cells of *Sphacelaria* the centrosome, according to STRASBURGER, is situated in a centrosphere at the center of an aster. Previous to mitosis it divides to two which take up positions at opposite poles. In *Stypocaulon* SWINGLE has shown that the centrosome, which lies close to the nucleus, divides, the daughter centrosomes diverging to opposite sides of the nucleus and occupying the spindle poles throughout mitosis. At all stages asters are present. SWINGLE is inclined to regard this centrosome as a permanent organ of the cell.

In the oogonium and segmenting oospore of *Fucus* FARMER and WILLIAMS (**24, 25**) described two centrospheres arising independently 180° apart. In the centrosphere they often observed several granules, but were inclined to attach no importance to them. STRASBURGER (**79**) reported definite centrosomes with asters all through karyokinesis; in the sporeling are stages which indicate that it is a dividing body. He regarded it as a permanent cell organ. In a more recent investigation YAMANOUCHI (**98**) demonstrates in the antheridium and oogonium two very definite centrosomes, which appear independently of each other, become surrounded by conspicuous asters, and occupy the spindle poles during karyokinesis. He further shows that when the sperm reaches the egg nucleus a new centrosome appears on the nuclear membrane at the spot where the sperm entered.

The centrosome of *Dictyota* has been dealt with by two investigators. MOTTIER (**69, 70**) states that in the two divisions in the tetraspore mother cell, in at least the first three or four cell generations of the sporeling and in all the vegetative cells of the tetrasporic plant, a curved rod-shaped centrosome with an aster occurs at the spindle pole. During the early phases of karyokinesis it divides, the daughter centrosomes passing to opposite poles. WILLIAMS (**91**) figures centrosomes and asters essentially like those described by MOTTIER. He also states that the entrance of the sperm causes a centrosome with radiations to appear in the egg cytoplasm.

WOLFE (**94**) found in his study of *Nemalion* that the spindle poles are always occupied, except possibly in the antheridial mitoses, by two heavily staining bodies which he considers centrosomes. They are surrounded by hyaline areas and apparently divide, but no radiations are present.

In *Polysiphonia* (YAMANOUCHI **96**) there are during the prophases of every mitosis two centrosome-like bodies in the kinoplasm at opposite poles of the nucleus. A little later the small bodies disappear, while the kinoplasm takes the form of large centrosphere-like structures without radiations. During the late anaphases these become indistinguishable. YAMANOUCHI believes that these structures are not permanent cell organs, but are formed *de novo* at the beginning of each mitosis.

In the tetraspore mother cell of *Corallina* (DAVIS **19**, YAMANOUCHI **99**) two deeply staining masses, or centrospheres, occur at opposite ends of the nucleus during the prophases of karyokinesis. They occupy the spindle poles and are surrounded by radiations. During the later anaphases they disappear and are formed *de novo* at the next division. No true centrosomes are present.

Among the fungi the best known centrosomes are those of the Ascomycetes. HARPER (**40, 41, 42, 43**) has described in the asci of *Peziza*, *Ascobolus*, *Erysiphe*, *Lachnea*, *Phyllactinia*, and other genera granular disc-shaped centrospheres surrounded by asters at the poles of the spindle. He regards them as permanent organs of the cell. GUILLIERMOND (**37, 38**) shows the presence of centrosomes and asters in several other genera. Especially interesting is the account of *Gallactinia succosa* given by MAIRE (**62**) and later by GUILLIERMOND (**39**). In the ascus of this form a single centrosome arises within the nucleus with a cone of fibers extending toward the chromatin. It divides to two which take up positions 180° apart at the nuclear membrane, at which time asters develop in the cytoplasm. FAULL (**26**) found that in *Hydnobolites* a large centrosome appears outside the nucleus during the prophases of karyokinesis. In *Neotiella* the spindle terminates in minute centrosomes with astral rays very faint or absent. In *Sordaria* he describes the centrosomes as disc-shaped while the cell is in the resting condition and round and smaller during division. The formation of the

spindle was not made out in these three forms. According to SANDS (**73**) the discoid "central body" or centrosome of *Microsphaera* divides with its aster to two which occupy the poles during karyokinesis. In *Humaria rutilans* Miss FRASER (**27**) saw at first two centrosomes lying near each other, each at the apex of a cone of fibers and surrounded by a very faint aster. These move apart and establish the spindle in the usual way. Centrosomes are also figured in *Ascobolus* and *Lachnea* (FRASER and BROOKS **29**). In *Otidea* and *Peziza vesiculosa* (FRASER and WELSFORD **28**) there are distinct centrosomes and asters. The figures given in this paper indicate that division of the centrosome occurs in the latter species. In a recent contribution CLAUSSEN (**16**) figures centrosomes with weakly developed asters in *Pyronema*. The origin of the spindle is not shown.

The first centrosome described in the liverworts was that of *Marchantia* by SCHOTTLÄNDER in 1893 (**75**). According to this observer the centrosome in the spermatogenous cells divides during the anaphases of mitosis, so that each daughter nucleus is accompanied by two. In the gametophytic cells certain minute bodies with radiations at the poles of the elongated nucleus and of the spindle are believed by VAN HOOK (**86**) to represent centrosomes.

Pellia has been the subject of four investigations dealing with the centrosome. In 1894 FARMER and REEVES (**23**) gave an account of mitosis in the germinating spore. They reported two centrospheres at opposite sides of the nucleus with conspicuous radiations but no true centrosomes. The centrospheres occupy the spindle poles and disappear during the telophases of division. DAVIS (**20**) studied the same mitoses and obtained similar results. He states, however, that the centrospheres fade out somewhat earlier. The account given by CHAMBERLAIN (**14**) agrees with these in the essential features. The structures are very distinct in the first mitosis but become less so in the succeeding ones. The most recent work is that of GREGOIRE and BERGHS (**33**). By using improved methods these investigators have found that neither in the resting cells nor during mitosis are there centrospheres or central corpuscles. The centrospheres described by other writers are

shown to be appearances due to the intersection of the very numerous astral radiations at a common point or region. The achromatic figure is derived entirely by the rearrangement of the cytoplasmic network.

As the centrosome becomes more widely known it becomes increasingly difficult to formulate for it any adequate definition. There is scarcely a single attribute common to all true centrosomes; nevertheless there are in general certain features which are fairly characteristic of them as they appear in plants and animals, most prominent among which are the position at the spindle poles with all that this implies, the possession of an aster, and the division to form daughter centrosomes. Because of many exceptions no one of these by itself will definitely determine the morphological nature of a structure possessing it, but when all of them are present we can no longer doubt that we are dealing with a true centrosome.

In a survey of the cilia-bearing structures of bryophytes, pteridophytes, and gymnosperms it is seen that in general the centrosome-like characteristics of the blepharoplast become less and less evident in passing upward through these groups, while the phenomena connected with the bearing of cilia become increasingly prominent. In the bryophytes the conflicting accounts leave us in some doubt concerning the early history of the blepharoplast, but in some cases at least it appears that centrosomes exist through several cell generations and after the last mitosis function as blepharoplasts. In those forms which show them only during the last division they occupy the spindle poles and behave as typical centrosomes. In the spermatids each simply elongates and bears two cilia. In the Filicales, as shown by YAMANOUCHI'S work on *Nephrodium*, the blepharoplast is limited to the last mitosis and does not exhibit the characters of a centrosome, having no division, no radiations, and only occasionally occupying the pole of the spindle. It elongates in intimate union with the spermatid nucleus and bears many cilia. In the gymnosperms the blepharoplast, although surrounded by prominent radiations, appears to play little or no active part in mitosis. In its subsequent behavior it differs widely from the blepharoplasts of the bryophytes and Filicales. After enlarging it becomes vacuolate and breaks up into many fragments, which

arrange themselves in a row and coalesce to form the cilia-bearing band.

The peculiar interest of the phenomena in *Equisetum* is here evident. Although limited to a single mitosis in the antheridium, the blepharoplast retains in its activities the most unmistakable evidences of a centrosome nature, and at the same time shows a metamorphosis strikingly like that in the cycads. In thus combining the main characteristics of true centrosomes with the peculiar features of the most advanced blepharoplasts, it reveals in its ontogeny an outline of the phylogeny of the blepharoplast as it is seen developing through bryophytes, pteridophytes, and gymnosperms, from a functional centrosome to a highly differentiated cilia-bearing organ with very few centrosome resemblances. In *Marsilia* the same pronounced centrosome behavior is shown through at least three cell generations, and in the formation of the cilia-bearing band the cycad situation is foreshadowed, though not to the marked degree seen in *Equisetum*. To the present writer these facts seem to constitute conclusive evidence in favor of the theory advanced by BELAJEFF and by IKENO, that the centrosome has gradually assumed the function of bearing cilia, at the same time losing the usual properties of a centrosome.

The points brought out in such a review are especially suggestive in connection with the conclusions to which WEBBER has been drawn by his studies on *Zamia* (**90**). This investigator emphasizes very strongly the view that the blepharoplast is a distinct organ functioning only as a cilia-former, and urges several objections to its centrosome nature. He points out that it differs from known true centrosomes in not being at the center of an aster at the poles and having no connection with spindle formation, in being limited to a single cell generation, in its great size, in its fragmentation, in its growth into a band, in its function of bearing cilia as far as plant centrosomes are concerned, and in its behavior in fertilization. Although the blepharoplasts of other plant groups are discussed, it appears that these conclusions must have been formulated largely through a consideration of the cycad situation. When the blepharoplast is regarded as an organ developing progressively through bryophytes, pteridophytes, and gymnosperms,

and is treated in the light of analogous phenomena in animals, much of the apparent force of these objections is removed.

In *Marsilia*, as BELAJEFF indicates in his fig. 7 (**7**), and in *Equisetum*, the blepharoplasts are surrounded during the early stages by asters, though these are very weakly developed. When they separate there appears a central spindle, forming with the asters an amphiaster so characteristic of animal cells. In *Equisetum* the radiations persist during the divergence of the blepharoplasts to opposite sides of the cell, and those on the side toward the nucleus remain as the achromatic portion of the karyokinetic figure. The weakness of the other rays or their failure to remain seems to be a matter of secondary importance in the light of spindle-forming activity of this sort. Furthermore, the figures given by zoologists indicate that the occurrence of an aster about the centrosome at the spindle pole is by no means universal in animal cells. In discussing this phase of the question IKENO (**54**) cites the work of MEVES and KORFF (**65**) upon the myriopod *Lithobius forficatus*, in which the spermatocyte centrosomes lie at a considerable distance from the spindle poles during mitosis. The figures given by MEVES and KORFF are strikingly like those of *Ginkgo* (HIRASÉ) and *Cycas* (IKENO).

It is true that the blepharoplast is, as a rule, limited to a single mitosis, but here we must remember the case of *Marsilia* where it is present during three, possibly all four, of the spermatogenous divisions, and also certain liverworts in which a similar condition has been reported. WEBBER accounts for the occurrence of blepharoplasts in all the spermatogenous cell generations in *Marsilia* by considering the latter potential spermatozoids, and thus regards the fact that they appear *de novo* in each cell generation only to disappear at the close of division as a support to his theory of the independent nature of the blepharoplast. If the cells between the central cell of the antheridium and the final spermatids are held to be potential spermatozoids, we should expect, as WEBBER points out, blepharoplasts or their rudiments to be present occasionally. Although these ideas are in accord with the conception of the blepharoplast as an organ *sui generis*, at the same time it does not seem to the present writer that they offer any necessary argument

against its centrosome nature, especially since such "rudiments" as are seen in the spermatogenous cells of *Marsilia* and probably certain liverworts are so remarkably centrosome-like. Moreover, many true centrosomes appear *de novo* in each successive cell generation only to disappear at the close of mitosis.

If the centrosome be an organ which has been practically eliminated from higher plants, we should not be surprised to see it retained, if at all, in different degrees in different plants, and in those cells in which it performs an important biological function, as other workers have suggested. WEBBER'S statement that no known plant centrosome has the function of bearing cilia is no longer without a possible exception, since JAHN (**56**) has seen the flagellum of the swarmer of *Stemonitis* growing out from the centrosome during mitosis, exactly paralleling what HENNEGUY (**44**) observed in an insect. That the bearing of cilia is the function which is to be held accountable for the retention of the centrosome in spermatogenous cells seems highly probable. After having lost the usual functions of a centrosome we might well find it appearing still later, in the spermatid itself, as WOODBURN (**95**) believes it does in certain liverworts. BELAJEFF'S view concerning the presence of these structures only in the spermatogenous cells is that every cell has its definite "dynamic center," but only in these cases is a staining substance present.

That growth into a band or thread does not deny the centrosome nature of an organ is shown by the great bodily elongation of the inner centrosome in the spermatozoon of *Helix* (KORFF **58**) and certain elasmobranchs (SUZUKI **82**, MOORE **68**). The rodlike centrosome of *Dictyota* and the discoid one of certain ascomycetes constitute a further argument against allowing the character of shape to enter into the definition of the centrosome.

Thus from the standpoint of the theory stated in the foregoing pages, the occurrence of secondary peculiarities developed in connection with cilia-bearing in the cycads and certain pteridophytes, such as large size, fragmentation, and growth into a band, does not distinguish the blepharoplast from the centrosome. This is emphasized by the fact that the first two of these features do not occur in the blepharoplasts of bryophytes and most pteridophytes,

but begin to appear in other members of the latter group, combined with earlier stages in all essential points centrosome-like.

Both WEBBER and STRASBURGER have pointed out that the blepharoplast, since it remains behind in the cytoplasm of the egg and does not meet the female nucleus, is inactive in fertilization, while in animals the centrosome brought into the egg by the spermatozoon plays a very important rôle in fertilization and in the first cleavage mitosis. They advance this as a further evidence that the blepharoplast and the centrosome are not homologous. We have seen that as the blepharoplast has become more and more highly differentiated in relation to the bearing of cilia, it has gradually lost the characters which would serve to mark it as a centrosome. The disappearance of activity during fertilization along with the other usual centrosome functions would be expected, if, indeed, the sperm centrosome of plants ever did take any active part in this process. In *Nephrodium* (YAMANOUCHI **97**) and probably many other pteridophytes and bryophytes the entire spermatozoid enters the egg nucleus, but it is highly improbable that the presence of the blepharoplast in these cases is necessary to fertilization. On the other hand, we cannot yet certainly conclude that a structure is entirely passive in fertilization merely because it does not reach the female nucleus or produce other striking visible effects. In any case it should be remembered that function is not that upon which we can base homology.

In denying the identity of the blepharoplast and the centrosome STRASBURGER (**80**) derives the blepharoplasts of bryophytes, pteridophytes, and gymnosperms from the thickened *Hautschicht* organs of algal swarm spores and gametes. This theory appears to have the support of current conceptions of phylogeny, but it leaves the remarkable behavior of the liverwort, *Marsilia*, and *Equisetum* blepharoplasts to be accounted for. That the *Hautschicht* organ seen in algae should assume, during the course of evolution, such centrosome-like characters, adding them at the earlier end of its life history, seems more difficult of comprehension than the theory stated in the foregoing pages—that the centrosome has gradually taken on the cilia-bearing function.

Through his work on *Marchantia* IKENO was led to state a view which might appear to lessen the contrast between the above two theories. He pointed out (**54**) the resemblance between the elongation of the blepharoplast along the plasma membrane of the *Marchantia* spermatid and the formation of the thickened portion of the *Hautschicht* in the algae as described by STRASBURGER and others, and concluded that this thickening has almost without doubt been derived from a centrosome ontogenetically or phylogenetically, that it is the metamorphosis product of a centrosome. His belief that the basal body in the swarm spore of *Hydrodictyon* is to be accounted for in a similar way was strengthened by the fact that TIMBERLAKE (**85**) observed what were evidently centrosomes at the poles of the spindles giving rise to the spore *Anlage*. In his later paper (**55**) IKENO is less inclined to include the algal *Hautschicht* organs in the same morphological category with the blepharoplasts of the higher plants, but places them in a class apart—"plasmodermal blepharoplasts."

In the light of our limited knowledge of the history of the blepharoplasts in algae it seems wisest to make this disposition of them for the present. Otherwise we should be compelled to assume their homology with those of the higher groups from which they differ so widely in origin, appearance, and general behavior. Since we can no longer remain in doubt concerning the centrosome nature of the blepharoplast of higher plants, this assumption would mean that the alga blepharoplast has lost all centrosome properties and now arises in the motile cell itself in a very modified manner, making it farther advanced in this respect than those of the higher groups, which we can hardly regard as probable. Before any final judgment can be rendered on this question more data must be gathered from the algae themselves, from those forms which show both centrosomes and blepharoplasts in their life histories.

The researches of MOORE (**68**), MEVES (**63, 64**), KORFF (**58**), PAULMIER (**72**), and several others have established beyond question the fact that the centrosome (or centrosomes) of the animal spermatid plays an important rôle in the formation of the motor apparatus of the spermatozoon, the axial filament of the flagellum

growing out directly from it. HENNEGUY (44) even observed cilia attached to the centrosomes of the karyokinetic figure in the spermatocyte of an insect.

In comparing the structures of the plant spermatozoid with those of the animal spermatozoon, BELAJEFF (5) regarded the blepharoplast, the thread to which it elongates, and the cilia of the former as homologous with the centrosome, middle piece, and tail, respectively, of the latter. The blepharoplast of *Chara* is included in this comparison in spite of the apparent difference in its mode of origin. STRASBURGER (80), although agreeing that the body at the base of the flagellum of the animal sperm is a centrosome, homologized only the axial filament of the flagellum with the blepharoplast. This comparison leaves both the cilia of the plant spermatozoid and the centrosome of the animal spermatozoon without counterparts, though a complete homology of this sort is by no means a necessity. The behavior of the centrosomes in the spermatid of *Helix* (KORFF 58) has made it evident that the axial filament of the flagellum is not a differentiation of the cytoplasm, starting at the centrosome, but is made up of the centrosome substance itself. Thus in comparing the blepharoplast to the axial filament its centrosome relationship is not entirely avoided. In a discussion of this question E. B. WILSON (92) regards the work of SHAW and BELAJEFF on *Marsilia* as establishing beyond question the identity of the blepharoplast and the centrosome. He considers the comparison of BELAJEFF as justified and concludes that "the facts give the strongest ground for the conclusion that the formation of the spermatozoids agrees in its essential features with that of the spermatozoa. . . . ."

The deeply staining bodies at the base of the flagella in other ciliated animal cells have also been investigated for further light upon this problem. That they correspond to centrosomes has been rendered highly probable by the work of HENNEGUY (44) and LENHOSSEK (60), while STUDNICKA (81) has obtained evidence apparently in favor of a contrary interpretation. This question must remain with others for further researches to clear up.

In the meantime it should be borne in mind that whatever interpretation is finally put upon the cilia-bearing structures of any

plant or animal group, it must not be forced upon those of all other groups. Since homologies are not determined by function, there is no necessity for expecting all of these organs to belong to the same morphological category. It is in the algae that the blepharoplast of plants at present stands most in need of elucidation. In the bryophytes, pteridophytes, and gymnosperms there can now remain no question that the blepharoplasts are all homologous structures, and that they are, to use IKENO'S expression, "ontogenetically or phylogenetically centrosomes."

Summary

1. In the early mitoses in the spermatogenous tissue of *Equisetum* there are no centrosomes, centrospheres, or asters.

2. A minute granule, surrounded by a weakly developed aster, appears in the cytoplasm near the nucleus in each of the cells of the penultimate generation. This granule divides to two, which become the blepharoplasts.

3. The two blepharoplasts, each with its aster, diverge to opposite poles of the nucleus. During the early stages of separation a distinct central spindle develops, so that an amphiaster is present.

4. The astral rays on the side toward the nucleus form two cones of fibers which, when the nuclear membrane breaks down, become the achromatic portion of the karyokinetic figure. The blepharoplasts occupy the poles.

5. During the anaphases and telophases of karyokinesis the blepharoplast enlarges, becomes vacuolate, and breaks up to a number of pieces. After further fragmentation these unite to form the cilia-bearing thread.

6. In the metamorphosis of the spermatid the nucleus and blepharoplast elongate spirally side by side, but have no connection other than that afforded by the undifferentiated cytoplasm.

7. The activities of the blepharoplast in *Equisetum*, taken together with the behavior of recognized true centrosomes in plants and analogous phenomena in animals, are believed to constitute conclusive evidence in favor of the theory that the blepharoplasts of bryophytes, pteridophytes, and gymnosperms are derived ontogenetically or phylogenetically from centrosomes.

The investigation here recorded was carried on under the direction of Professor JOHN M. COULTER, Dr. CHARLES J. CHAMBERLAIN, and Dr. W. J. G. LAND, to whom the writer wishes to express his sincere thanks. He is also greatly indebted to Dr. SHIGÉO YAMANOUCHI for many helpful suggestions.

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EXPLANATION OF PLATES VII AND VIII

All figures were drawn at the level of the table with the aid of an Abbé camera lucida under a Zeiss apochromatic objective 2 mm. N.A. 1.40, with compensating ocular 18. They have been reduced one-third in reproduction, and now show a magnification of 2533 diameters.

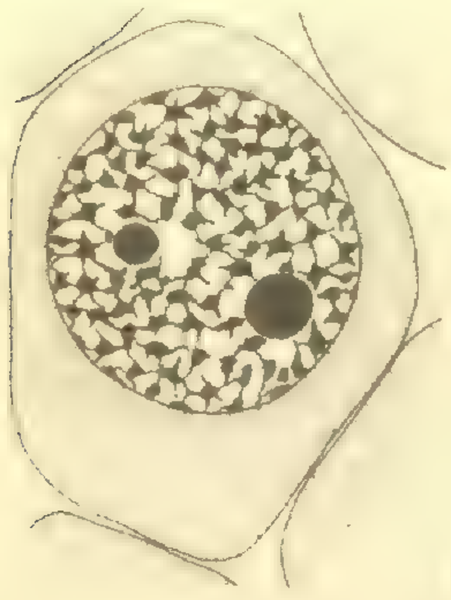
PLATE VII

FIG. 1.—Cell of penultimate generation rounding off.

FIG. 2.—Deeply staining body with faint aster present in cytoplasm.

FIG. 3.—Division of small body in cytoplasm.

FIG. 4.—Two blepharoplasts formed by division of the original body.



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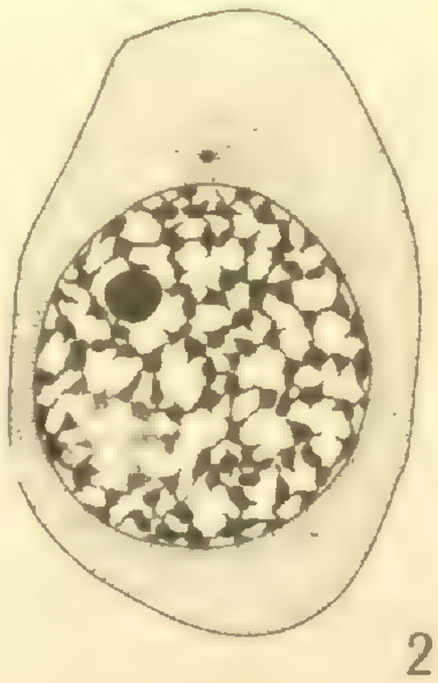

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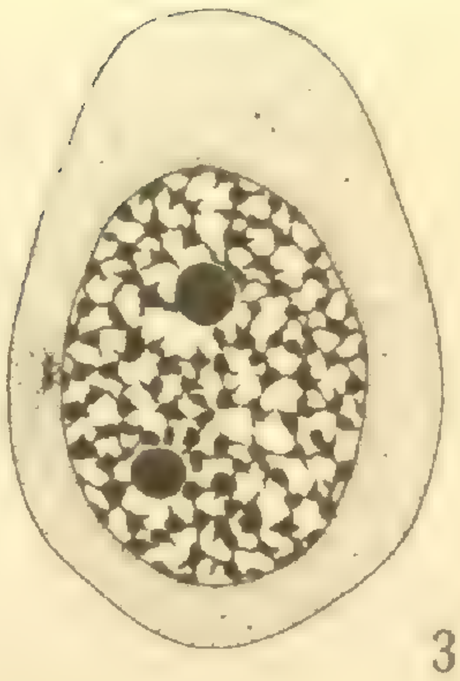

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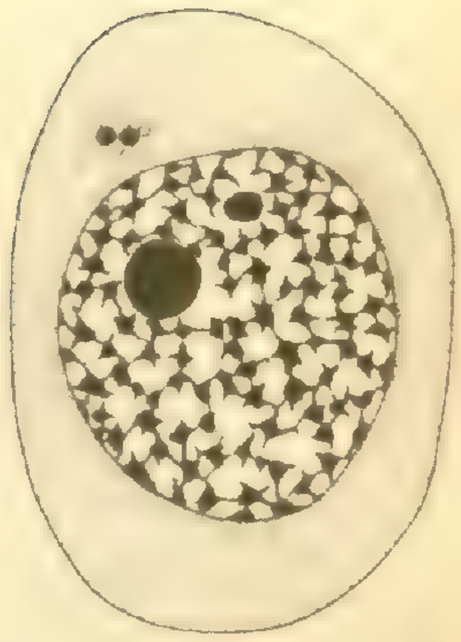

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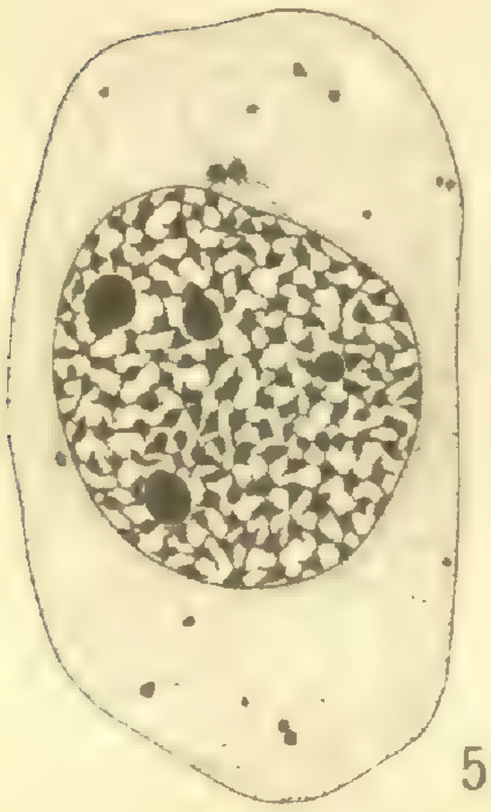

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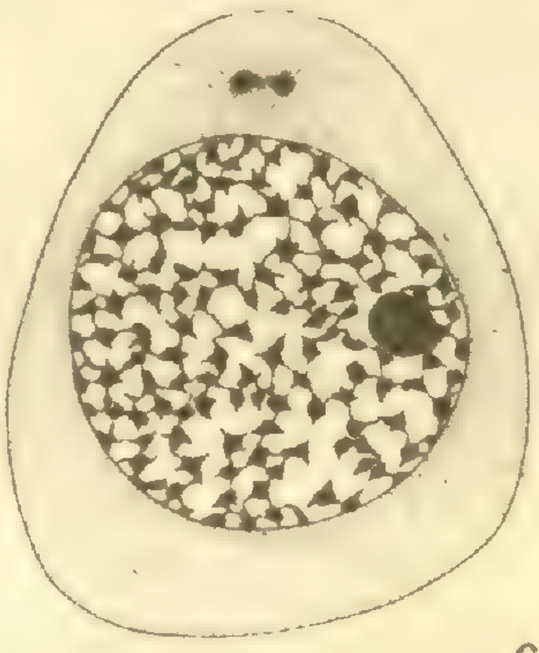

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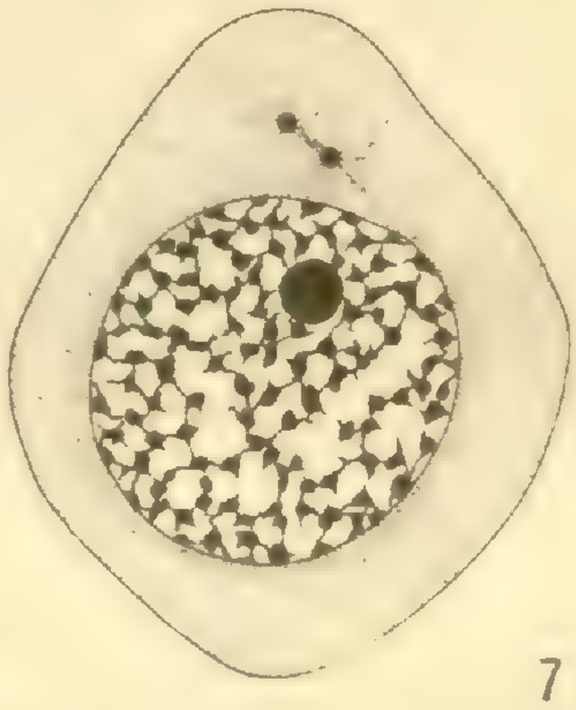

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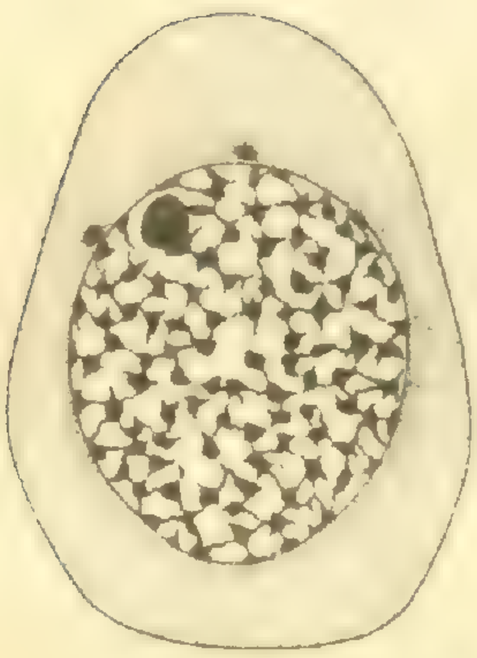

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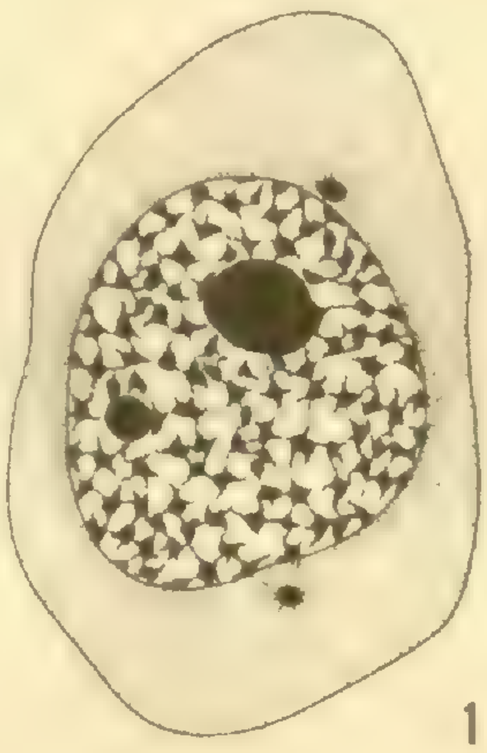

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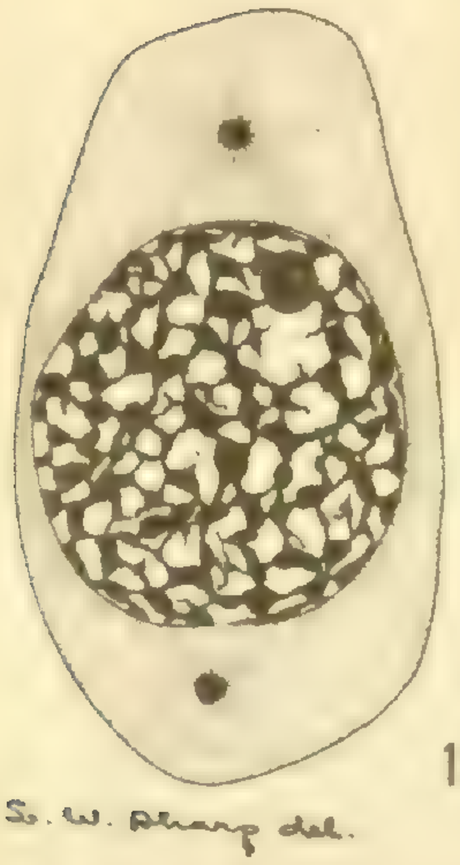

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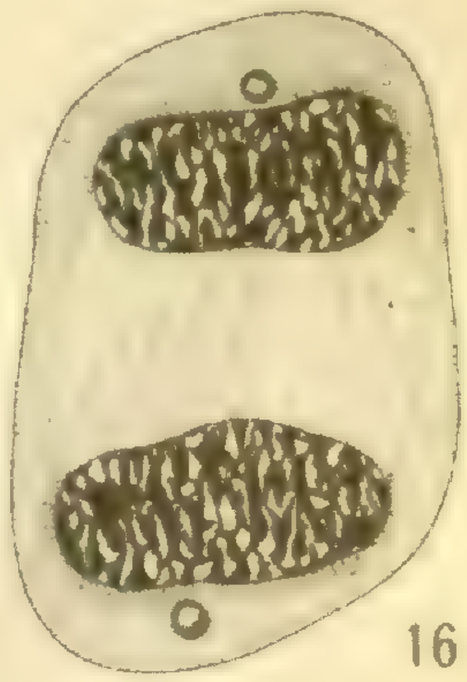

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S. W. Sharp del.

SHARP on EQUISETUM

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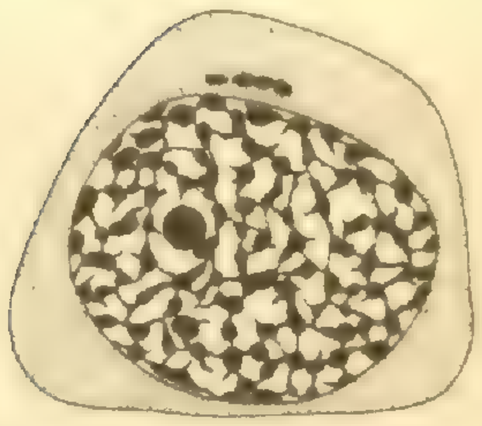

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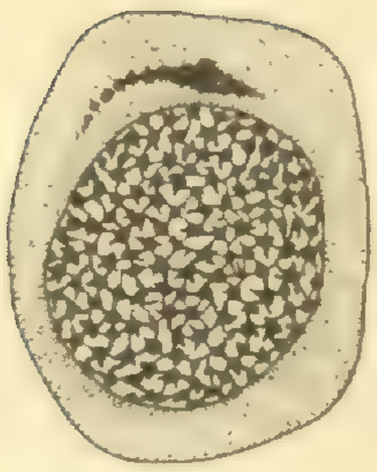

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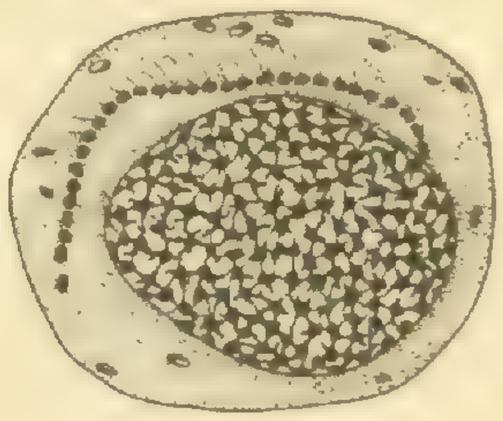

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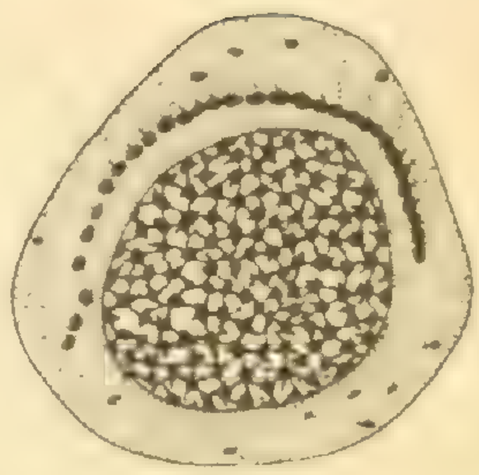

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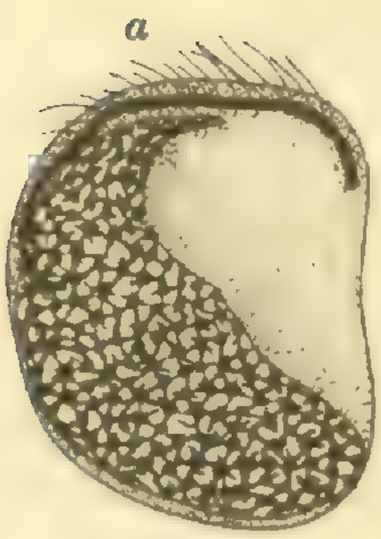

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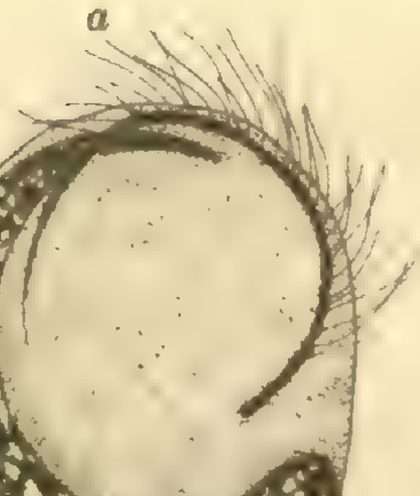

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S. W. Sharp del.

SHARP on EQUISETUM

FIG. 5.—Blepharoplasts at upper side of nucleus; other single and paired bodies present in cytoplasm; exceptional condition.

FIG. 6.—Blepharoplasts beginning to separate; central spindle present; the radiations on the side toward the nucleus form a distinct cone.

FIG. 7.—Later stage; no cone of rays present.

FIG. 8.—Still later stage; central spindle fading out.

FIGS. 9–12.—Stages in the divergence of the blepharoplasts.

FIG. 13.—Blepharoplasts lying at a greater distance from nucleus; the radiations on the side toward the nucleus form two well marked cones; the chromatin network becoming coarser.

FIG. 14.—Spirem stage: nuclear membrane beginning to break down; astral rays much shorter.

FIG. 15.—Late prophase: the spindle fibers have been formed from the radiations of the blepharoplasts, which occupy the poles.

FIG. 16.—Telophase: blepharoplasts have enlarged and become vacuolate.

PLATE VIII

FIG. 17.—Pair of spermatids differentiated: blepharoplasts have the form of irregular rings; plastids present in cytoplasm.

FIG. 18.—Spermatid: blepharoplast beginning to fragment.

FIG. 19.—Blepharoplast broken up to several pieces.

FIG. 20.—Granules formed by fragmentation of blepharoplast beginning to draw out into a row; nucleus again in resting condition.

FIG. 21.—Blepharoplast granules arranged in a long row; cilia beginning to grow out from them; plastids present.

FIG. 22.—Blepharoplast granules fusing at right end of chain; still separate at left end; degenerating plastids in cytoplasm.

FIG. 23.—Blepharoplast now a continuous thread; cilia partially developed; nucleus beginning its metamorphosis.

FIG. 24.—Portion of a similar cell viewed from the direction *a*, showing proximity of nucleus and blepharoplast; cilia not drawn.

FIG. 25.—Later stage: nucleus and blepharoplast have elongated spirally; chromatin network very coarse.

FIG. 26.—Entire cell similar to that of fig. 25 viewed from the direction *a*, showing independence of nucleus and blepharoplast; cilia not drawn.

FIG. 27.—Section of similar cell in plane *ab*: *n*, nucleus; *b*, blepharoplast; cilia not drawn.

FIG. 28.—Mature spermatozoid still in antheridium: the blepharoplast makes 1.4 turns, the nucleus 0.7 of a turn; deeply staining globules in cytoplasm near nucleus.

FIG. 29.—Smaller spermatozoid in another antheridium, viewed from a different direction.

FIG. 30.—Spermatozoid fixed in the swimming state over osmic fumes: the dark spiral band bearing the cilia is the blepharoplast; the lighter, homogeneous portion the nucleus; the vacuolate portion the cytoplasm; length exclusive of cilia, 19.7 μ.

THE PRIMARY COLOR-FACTORS OF LYCHNIS AND COLOR-INHIBITORS OF PAPAVER RHOEAS[1]

GEORGE HARRISON SHULL

The frequency with which the presence of hereditary characters is dominant over their absence naturally suggests that inhibiting factors may be operating when the reverse relation appears to exist, as when the hornless character of polled cattle dominates over horns, and the "smooth" character over the "bearded" in wheat, oats, etc. Some writers (DAVENPORT, BATESON, PUNNETT) have even taken the extreme view that dominance is in all cases a criterion of "presence." That this position is untenable I have shown several years ago (SHULL **11, 12**), and CASTLE (**2**) also opposes such an idea, calling attention to WOOD'S well known sheep hybrids (WOOD **15**), in which the horned condition is dominant in the male and hornlessness in the female offspring from the same cross, as a proof that no such sweeping generalization is permissible. It may be granted, however, that presence is *usually* dominant, and that the dominance of the apparent absence of a character is probably in most cases, but not in all, the dominance of an inhibiting factor over its own absence. It is only necessary to keep the mental reservation that in any single instance of a putative inhibitor another hypothesis is always available, namely, that the gene for the character that is supposed to be inhibited, when existing singly as in the heterozygote, may be nearly or quite incapable of reaching the threshold of visible expression.

Both of the characters mentioned above by way of example—the polled condition in cattle and the lack of long awns in wheat—are structural characters. When a *color*-character is inhibited, the

[1] Under the title "Inhibiting factors in *Lychnis* and *Papaver*," this paper was read before the Botanical Society of America, Washington, D.C., December 28, 1911. The change of title and slight changes in the text have been rendered necessary by the discovery that the purple-flowered male parent of family 10201 discussed below was probably heterozygous in both the primary factors for color. This discovery in no wise affects the general considerations presented in the paper as read, but it withdraws *Lychnis dioica* for the present as an example of dominant white.

result is a "dominant white" if the inhibition of all pigmentation is practically complete, or there may result parti-colored forms exhibiting various color-patterns, or the dominance of what appears to be a lower grade of pigmentation over a higher grade when the inhibition is localized or otherwise incomplete.

One of the earliest known and most familiar examples of dominant white is found in the plumage of domestic fowl, in most breeds of which white is epistatic to all colors, but not always quite perfectly so. It was soon found, however, that not all of the plumages of white fowl are of the same nature, for the "Silkie" fowl's white plumage is recessive to colors. Dominant and recessive whites have been discovered in a number of other cases, both in plants and in animals. BATESON (**1**, p. 105) and GREGORY (**7**) found that white-flowered primulas with red stems are dominant whites, while those with green stems are recessive whites;[2] KEEBLE, PELLEW, and JONES (**9**), and Miss SAUNDERS (**10**) have demonstrated dominant and recessive whites in *Digitalis purpurea;* and EAST (**4**, pp. 81 f.) has shown that an inhibitor for blue aleurone-color exists in some maize plants though absent in others.

In many cases, perhaps generally, the inhibition is not quite complete, and dominant whites are often distinguishable by the possession of patches or washings of color not found in recessive whites. Similar incompleteness of action of inhibitors is seen in the occasional appearance of rudimentary horns or "scurs" in pure-bred polled cattle, in the development of a few feathers on the legs of pure clean-legged fowls, the production of short awns or "beards" on "smooth" wheat, oats, etc.

Not only are there dominant and recessive whites, but there are also different kinds of these, dependent upon the fact, now well known, that the same visible effect may be attained in various ways. It has been demonstrated that pigmentation is generally due to the interaction of at least two independent factors. When only two such factors are required, e.g., *C* and *R*, there may be three kinds of recessive whites, one lacking *C*, one lacking *R*, and

[2] While this is the general rule, KEEBLE and PELLEW (**8**) have found exceptions in the variety "Pearl," which has dominant white flowers and green stems, and in "Snow King," in which both dominant and recessive whites were found associated with dark red stems.

one lacking both *C* and *R;* and each of these whites will behave differently in certain crosses, though all are recessive to colors and may be quite indistinguishable from one another when pure-bred. Individuals lacking either *C* or *R*, when crossed with other individuals having the same genotypic constitution, or when crossed with individuals of the third type, which lack both *C* and *R*, will produce only white offspring; but when recessive whites of the first two types are crossed together, the complementary factors, *C* and *R*, necessary for the production of color, are brought together and a colored F_1 results, as exemplified by the classic case of "Emily Henderson" sweet peas, in which two white-flowered plants, differing externally only in the form of the pollen-grains, produced "reversionary" purple offspring when crossed together. Many similar "reversions" have been discovered by experimental breeders in a considerable number both of plants and of animals, and the old riddle of "reversion on crossing," exemplified by these phenomena, has been given a satisfactory solution in the "factor hypothesis." In so many organisms have different kinds of recessive whites been found, that their discovery in additional species no longer occasions surprise.

Less is known of the chemistry of dominant whites, but it is conceivable that these may also be of several kinds. It is plain that any pigment which is readily converted into an allied colorless compound would give a basis for a dominant white in which the pigment nucleus coexists with a factor which changes it to its colorless derivative. A suggestive illustration *in vitro* of such a reaction is the ready reduction of indigo blue ($C_{16}H_{10}N_2O_2$) in alkaline solutions to indigo white ($C_{16}H_{12}N_2O_2$). SPIEGLER (**14**) believed that he had succeeded in isolating a "white melanin" from white wool and white horsehair, and while GORTNER (**5, 6**) has been unable to confirm SPIEGLER'S conclusions in this regard, the general type of reaction suggested by SPIEGLER may be retained as possibly explaining some cases of dominant white. GORTNER (**5**) has proposed a very different hypothesis, namely, that as melanin is the product of an oxidase acting on a chromogen (tyrosin), dominant whites may be the result of anti-enzymes which inhibit the action of the oxidase. The same hypothesis is applicable to

the widely distributed plant-pigment anthocyanin, whose method of origin appears to be in essential agreement with that of melanin. More recently GORTNER (**6**) has shown that anti-enzymes are not necessary for the inhibition in question, as the oxidizing action of tyrosinase is prevented by the presence of small quantities of such relatively simple *m*-dihydroxyl phenolic compounds as orcin, resorcin, and phloroglucin. GORTNER shows that on the basis of his investigations a satisfactory explanation can be given of those rare cases in which a white is dominant in some crosses and recessive in others, as apparently exemplified by the Shirley poppies described below.

I have been making numerous crosses among strains of *Lychnis dioica* L., and during the past six years have grown about 660 pedigreed families of this species. Nearly 300 of these families have resulted from matings between white-flowered individuals, many of the matings having been arranged for the specific purpose of finding different kinds of whites possessing complementary color-factors. Until the past summer (1911) all of these crosses between white-flowered parents have given uniformly white-flowered progenies,[3] and a similar number of crosses between white and colored individuals have invariably shown the whites to be recessive to colors, though they differed genotypically in that some of the whites carried a factor for reddish-purple and others a factor for bluish-purple, the red being epistatic to blue.

With the bringing in of two new strains of *Lychnis dioica* from their native habitats in Germany (for seeds of which I am indebted to Dr. BAUR), I have realized the complementary factors for color for which I had been looking thus far in vain.[4]

[3] The several purple-flowered individuals from white-flowered parents, mentioned in an earlier paper (SHULL **13**), appear now to have been plus-fluctuants of a "tinged white" which had not been recognized as such at the time that paper was written. They have no bearing on the problem of complementary color-factors here under consideration.

[4] That the several kinds of recessive whites exist among my Cold Spring Harbor strains, though I have not yet made a mating among them between two whites which resulted in a purple-flowered F_1, is sufficiently demonstrated by the facts presented in my earlier paper. My failure thus far to secure a purple-flowered F_1 from two whites among these strains must be due to the mere chance that I have not selected whites from the proper families.

These two forms of *Lychnis* from Germany are with apparent good reason classified by German taxonomists as distinct species, the white-flowered form being called *Melandrium album* Garcke, and the purple-flowered form *M. rubrum* Garcke. *Melandrium album*, as it appears in my cultures, has relatively narrow, spatulate, moderately ascending rosette-leaves of a rather dull dark green; the corollas are white, slender, and long-exserted from the calyx-tube; the styles are long and slender, with inconspicuous stigmatic papillae. The plants are easily grown as annuals by early sowing. *Melandrium rubrum* Garcke, grown under the same conditions, has the rosette-leaves broader, with more rounded apices; the leaves are nearly horizontal, a little darker green, and more shining. The corollas are reddish-purple, shorter, scarcely extending beyond the mouth of the calyx; the styles shorter and relatively heavy, with prominent stigmatic papillae. A very small percentage of the plants are forced to bloom as annuals, even when seeds are sown early in February. In so far as visible characters are concerned, these two forms have shown but slight fluctuations, except that in *M. album* the calyx varies from plain green through green striped with purple to a rather deep dull crimson. They have kept quite distinct from each other in regard to the characteristics enumerated, but because they breed together with undiminished fertility and because I have many other strains showing similar differences and various degrees of intermediacy, I must continue for the sake of convenience the use of the Linnean name (*Lychnis dioica*) for the entire aggregation. To what extent the other forms in my cultures may have been derived from hybridizations between *M. album* and *M. rubrum* cannot be surmised, but all strains which I have thus far found in America have presented one or more characteristics which are not directly traceable to either of the German forms, nor obviously derivable from them by recombinations of their characters. For instance, my original material of this species, collected at Cold Spring Harbor, has considerably lighter green foliage than either *M. album* or *M. rubrum*, and from the vicinity of Harrisburg, Pa., I have secured a "chlorina" (CORRENS **3**) variety having light yellow-green foliage.

Three crosses were made in 1910 between the German *Melan-*

drium album and my original white-flowered strain from Cold Spring Harbor. Two of these families (10200 and 10202) were the result of crossing two different German white-flowered females with pollen from a single Cold Spring Harbor white-flowered male. Both of these matings produced only white-flowered offspring, totaling 182 individuals. The young seedlings were indistinguishable from Cold Spring Harbor seedlings of the same age, but later they became darker green and were intermediate between the parents. A third family (1068) was essentially reciprocal to the two just described, being produced by crossing a female sib of the male used in 10200 and 10202 with pollen from a German white-flowered male. The 77 offspring were vegetatively indistinguishable from the reciprocal families, but the flowers were all reddish-purple. These different results in supposedly reciprocal crosses probably indicate that there was an unsuspected heterogeneity in the German strain. That the difference was due to heterogeneity in the Cold Spring Harbor parental family is rendered improbable by the fact that a mating (1060) between the female used as the mother of 1068 and the male used as the father of 10200 and 10202 resulted in a progeny of 73 white-flowered plants. It is unfortunate that a similar check was not applied to the German plants entering into these families, by also crossing them together. The only cross (10203) made between two specimens of *M. album* resulted in 84 offspring, all white-flowered. The mother of this family was also the mother of 10202, but the father was not the same as the father of 1068.

Several crosses were also made between the purple-flowered German *Melandrium rubrum* and my Cold Spring Harbor strains, both white-flowered and purple-flowered. Families 1092 and 1093 were produced by crossing a single white-flowered female of the Cold Spring Harbor strain with two males of *M. rubrum*, one derived from seeds collected at Furtwangen in the Schwarzwald, and the other from Oefingen in Baden. A female sib of the last-mentioned plant (i.e., from Baden) was crossed (10204) with pollen from a white-flowered sib of the mother of families 1092 and 1093. It represented a cross, therefore, as nearly reciprocal to 1093 as is possible in dioecious material. Two other families

(10206 and 10207) were produced by crossing two females grown from the Baden seeds with pollen of a single pure-bred purple-flowered male from Cold Spring Harbor. As *Melandrium rubrum* has reddish-purple flowers and as this color has been shown to be epistatic to bluish-purple (which may have been carried as a latent character by the white-flowered plants), there was no reason to expect that the F_1 progeny of any of these five crosses would present any noticeable difference in flower-color from that of their *M. rubrum* parent. This expectation was realized, the 262 offspring from these crosses all having reddish-purple flowers. The young plants in these families were generally indistinguishable from pure-bred *M. rubrum*, but later they differed by being notably more vigorous, having enormous rosettes of broad, shining, dark-green leaves. They were also much more easily grown as annuals by early sowing, being in this regard intermediate between the parents. Almost all of the hybrids were blooming by the middle of July, before the first flowers of any pure *M. rubrum* had opened.

Compared with these crosses between *Melandrium rubrum* and the Cold Spring Harbor plants, a cross of *M. rubrum* with *M. album* gave a totally different and unexpected result. A mating between a female of the white-flowered *album* and a purple-flowered male *rubrum* produced an F_1 (10201) consisting of 23 white-flowered individuals and 3 (probably 4) purple-flowered ones. The white-flowered plants were unlike either parent in vegetative characters, having relatively short, sharp-pointed, grayish-green leaves which were strongly ascending in the fully developed rosette, while both parents have long, spreading, dark-green leaves. The flowers were not only white like those of their white-flowered mother, but they were also nearly identical with them in form. It was noted that rarely some of the flowers became faintly and unevenly streaked and washed with purple just as they were fading, a feature never observed in the flowers of any of my other white-flowered plants. These white-flowered hybrids were a little later in blooming than their white-flowered parent, but were still easily induced by early sowing to behave as annuals. The purple-flowered offspring of this cross were of an altogether different character, and were not readily distinguishable in rosette and

floral characters from their purple-flowered male parent. They were also like pure *M. rubrum* in not blooming until late in the season. One plant having a rosette identical with those of the three purple-flowered specimens remained a rosette, but will doubtless have purple flowers if it survives the winter.[5]

Why there should be this segregation of types in the F_1, and why one of these types should so completely resemble the male parent, while the other type was goneoclinic to the female parent, though abundantly distinct from it in the rosettes, are mysteries. Perhaps this unexpected segregation of characters in a putative F_1 is further evidence of the heterogeneity of the *M. album* material. If the white-flowered mother were heterozygous in a dominant white factor, the expected result of a cross with *M. rubrum* would be 3 white-flowered to 1 purple-flowered, or in this particular family 20 white-flowered to 7 purple-flowered, to which expectation the observed result is in sufficiently close agreement considering the small number of individuals. The same result would be attained if the *rubrum* parent were heterozygous in respect to both the primary factors for color, *C* and *R*, it being assumed that the *album* parent lacked both these factors. No other evidence of heterogeneity in *M. rubrum* has yet appeared in my cultures. It should be remarked that neither of these German strains had been pedigreed in controlled cultures, but were simply collected in separate regions in nature, so that questions as to their genotypic purity are legitimate.

In the derivatives of the corn-poppy (*Papaver Rhoeas* L.), among which are the dainty and beautiful "Shirley" poppies of our gardens, color-inhibitors are also found. According to his own statement, Rev. W. WILKS was first induced to pursue the course of selection, which resulted in the strain known as the "Shirley poppies," by discovering a bud-variation on a wild corn-poppy growing in a corner of his garden. Several flowers on this plant differed from the rest in having petals with a narrow white margin. Such a white margin is now a frequent feature of garden poppies, and when appropriate crosses are made, it is found that the presence

[5] Note added June 5, 1912. This plant is now blooming and has purple flowers as predicted.

of a margin is dominant over its absence. It is probable, therefore, that the white margin is due to the presence of an inhibitor whose action is localized in the margins of the petals.

In 1911, among 73 pedigreed families of *Papaver Rhoeas* grown at the Station for Experimental Evolution, 45 resulted from crosses between plants of which the presence or absence of a margin had been recorded, and of which a goodly proportion of the offspring were capable of being similarly recorded. The rest either had one white-flowered parent whose possession (or lack) of a margin could not be determined by inspection, or for some other reason one or both parents or the offspring could not be safely characterized with respect to margins. Of the 45 families having the margins of parents and offspring recorded, 3 represented crosses between plants both of which had margined petals, 17 were from crosses between one margined and one unmargined parent, and 25 resulted from matings between plants none of which had margined petals. The three families from matings between margined parents consisted of 236 individuals, including in each family a mixture of plants with margined and with unmargined petals. Records of the margins were often impossible, owing to the interference of other factors not yet fully investigated, so that the numbers of each type of offspring have no special significance in the present connection and they will be reserved for discussion at another time.

Of the 17 families produced by mating plants with margined and with unmargined petals, 12 were composed of a mixture of plants, some with margins and some without, 3 contained only plants with unmargined petals, and in 2 families practically all of the individuals had margins. With margins dominant over their absence, only two kinds of families were to be expected from this type of mating, namely, all margined if the margined parent chanced to be homozygous, and mixtures of plants with margined and unmargined petals if the margined parent was heterozygous. The three families (10272, 10273, 10274) in which no margins appeared, though one of the parents had a margin, are exceptions. One margined individual was the mother of all three of these exceptional families. The records show that this plant differed

from the usual type, the margin being in this case red-violet[6] instead of nearly white. Whether this red-violet margin was a purely somatic modification of the dark-red body-color, or whether it was germinal, it was clearly of a different nature from the white margins involved in the other families.

In the two families (10287, 10289) whose margined parents were evidently homozygous, a small number of plants were recorded without margins. These exceptional plants occurred among those set into the garden, while larger numbers of plants from the same families, which were grown to maturity in pots in the propagating-house, were all margined. In family 10287 there were 6 plants with unmargined petals among 40 grown to maturity in the garden, and none among 133 which flowered in pots, and in family 10289 one was noted as unmargined among 47 plants in the garden and none among 83 which developed in pots. However these seven unmargined specimens are to be accounted for, it is clear that each of these families is the offspring of a homozygous margined parent.

In the 25 matings between plants, neither of which possessed margined petals, there appeared only 15 plants with margins among a total of 1402 offspring, and in a number of those recorded as margined the margin was merely a trace of lighter color of more or less doubtful character. Only in one family (10291) were the margins unmistakable, and in this family the margined plants occurred only among those which were retained in the greenhouse. Of 21 which matured in the garden none had margins, while among 99 which flowered in pots in the greenhouse there were 10 with margins, several having only a trace, while others had well marked white margins 2 mm. wide—in one plant 3 mm. wide. No attempt need be made at present to account for these few margined plants, for their number is too small to vitiate the conclusion that the unmargined condition is recessive, and that typically all the offspring of two unmargined parents are unmargined.

The most interesting matings in which margins were involved

[6] The color-nomenclature adopted in this paper is based on the spectrum colors, as arranged in the Milton Bradley system. Exact shades and tints have been recorded, but for the sake of simplicity these have not been reproduced here.

were those in which the wild poppy was crossed with its garden derivatives, for as already noted the margin is a new character which does not normally occur in the wild poppy. In the two families representing such matings, the wild poppy was used as the mother in 10298 and as the father in 10310. Both families consisted of mixtures of margined and unmargined plants, showing conclusively here also that margined petals is a dominant character, since the wild plants are certainly homozygous in the lack of such margins. The dominance of the margined condition of the garden poppies over the unmargined condition of their wild prototype is in marked contrast to all the other color-characters of *Papaver Rhoeas* yet investigated, for the dark red-orange body-color[7] of the wild poppy is epistatic to all the body-colors presented by the numerous garden forms. If dominance were a secure criterion of the presence of a gene which is absent in the recessive type, these results would indicate that while the various body-colors of the garden forms originated as retrogressive mutations, i.e., by losses of characters, the white margins of the petals represent a progressive mutation through the addition of a gene which inhibits the development of color in that region. Doubleness also proves to be dominant over the single type of the wild poppy, and, on the basis of the same assumption, would have to be classed as a progressive mutation. I cannot forbear, however, to repeat the caution that dominance does not necessarily demonstrate the progressiveness of a mutation, since the alternative hypothesis, mentioned above in the first paragraph, allows for the dominance of a character which has originated by a retrogressive mutation.

There is still one other color-inhibitor (possibly several) in the derivatives of *Papaver Rhoeas*, which is in some respects more noteworthy than that which produces the white margins. This affects the body-color of the petals, producing what is essentially a dominant white, though in this case the inhibition is not usually complete and the flowers often show some irregular striation of dull violet, reddish, or bluish color on the petals, especially in the presence of purple stamens.

[7] By the expression "body-color" it is intended to indicate the color of the general intermediate region of the petals as distinct from "center" (proximal) and "margin" (distal).

A single white-flowered plant with yellow stamens was crossed in 1909 with three red-flowered plants (yielding families 10275, 10281, 10282) and with two plants having dull striations on the petals (families 10280, 10283), and the offspring of these five matings were generally white or whitish-flowered. Of 559 plants in these families only 25 were neither pure white nor white with traces of reddish color, and of these 25, all that had a full red (i.e., not striated) parent were lighter in color than that parent. These fully pigmented offspring may simply represent minus-fluctuations in the action of the inhibitor derived from the white-flowered parent. If this is the correct interpretation of these few plants with colored flowers, it should be possible to secure from them progenies displaying the presence of the inhibitor though it be invisible in both parents. While I have as yet grown no offspring from the colored plants of these families, I have two other families (10270, 10308) in which the same whitish offspring have appeared, though both parents in each case were fully pigmented. Family 10270 was produced by mating two dark-red parents which were sibs in a family consisting of red, red-orange, pink (light violet-red), and white. The progeny of these two dark-red plants consisted of 68 white or whitish and 70 pigmented, the latter often striated and generally much less intensely pigmented than either parent. Only two of the offspring showed as deep shade as that of their parents. The parents of family 10308 were also red-flowered sibs in a family containing red, red-orange, pink, and white. They were considerably lighter red than the parents of 10270, but were fully and evenly pigmented. Their offspring consisted of 80 white- and whitish-flowered plants and 13 with pigmented flowers, none of which were as deeply pigmented as either parent, and several of which showed the peculiar striation which seems to be one of the manifestations of the inhibitor believed to be operating in these crosses. Similar results were obtained in seven families (10266, 10273, 10274, 10297, 10303, 10305, 10311) produced from mating together two plants with striated petals, or a striated with a plain red, and only in one family, containing three individuals (10268), did the "dominant white" fail to manifest itself in progenies from matings of this character. In the latter family a

cross between a light-red and a striated individual produced three offspring, all with flowers slightly darker red than those of their red-flowered parent. Considering the complexity of some of these families, this number of individuals is entirely inadequate for the deduction that family 10268 was really exceptional.

While I have laid no emphasis thus far on the fact, it may have been noted that all of these poppy-families in which a "dominant white" has made its appearance have been derived from red or striated parents, never from red-orange or pink (light violet-red). It seems that the factor under discussion is not a general inhibitor of color but only of pure spectrum-red. The following facts seem to prove this: The same white-flowered plant with yellow stamens which we have seen producing white-flowered progenies when mated with red (families 10275 and 10281) was also mated with two homozygous pink-flowered plants (families 10277 and 10278) and a homozygous red-orange plant (10279) and in all of these three crosses the white-flowered parent proved to be a recessive white. Families 10277 and 10278 consisted of 43 pink-flowered and 25 red-flowered plants, and 10279 contained 226 red-orange-flowered plants and 1 red-flowered. Not a single individual in any of these three families had white or whitish flowers. In keeping with these results are families in which striated plants were mated with pink (10295) and red-orange (10301), for in neither of these families appeared a white-flowered offspring or one with striations, 10295 yielding 37 pink-flowered and 33 red-flowered and 10301 giving 22 which were red-orange and 5 intermediate between this and red.

The occurrence of many red-flowered plants in these families, when one of the parents supposedly contained an inhibitor for red, is not satisfactorily explainable on the assumption made above, that there is a single inhibitor for red whose effectiveness fluctuates to such an extent that its presence may not be detected in its extreme minus-fluctuations. An alternative hypothesis may be suggested, which must await further experimentation for its confirmation or rejection. If there be two factors, A and B, which are ineffective when existing apart from each other, but which become an inhibitor when acting together, the observed

results could be explained by assuming that in those matings which produced whitish-flowered offspring, the one parent possessed *A*, the other *B*, while in those matings in which a fully pigmented progeny was produced, the two parents had the same factor—either both *A* or both *B*—or else one of them lacked both *A* and *B* and the other parent lacked one of them. The occurrence of fully pigmented individuals in association with "dominant whites" need not then be minus-fluctuations of a single inhibitor, but might be the result of segregation of inhibiting factors, one or more of which were heterozygous in one or both parents.

Summary

Dominant and recessive whites have been discovered in a number of different plants and animals. Both the dominant whites and the recessive whites may be of different kinds, though externally indistinguishable.

Dominance does not necessarily indicate presence of an added gene, but when the absence of a character appears to be dominant over its presence, the action of an inhibiting factor may usually be inferred. An alternative hypothesis is always available, however, which should prevent a too dogmatic assertion that dominance is synonymous with presence.

A white-flowered form (*Melandrium album*) of *Lychnis dioica* L. from Germany, when crossed with the purple-flowered form (*M. rubrum*) from the same country, produced 23 white-flowered and 4 purple-flowered offspring, but in certain crosses with a white-flowered strain derived from plants growing at Cold Spring Harbor, the German white-flowered plants produced purple-flowered offspring in the F_1, in other crosses only white-flowered offspring were produced.

In the "Shirley" poppies (*Papaver Rhoeas* L.), the presence of a white margin of the petals is a dominant character and is probably due to an inhibitor limited in its effective action to the margins of the petals.

These white margins and doubleness of the flowers are the only characters in the garden poppies which were found dominant over the corresponding characters of the wild type from which they

were derived. They may represent the results of progressive mutations, but here again caution is necessary because of the alternative hypothesis.

There is also an inhibitor which affects the body of the petals in the "Shirley" poppies, producing what is essentially a dominant white, though the inhibition is often very imperfect, in which case the flowers are more or less washed and striated with color, though generally whitish.

This supposed inhibitor was evident only in crosses involving at least one red-flowered or striated parent. The same white-flowered plant which was a dominant white in crosses with red-flowered and striated plants was a recessive white in crosses with pink-flowered and red-orange-flowered plants.

In several cases red-flowered plants crossed together produced a whitish progeny and a similar result was produced when two striated plants were mated or when striated was crossed with red.

Two hypotheses to account for these facts are considered: (*a*) that there is one inhibitor affecting only the pure spectrum-red and having no effect on pink and red-orange; the minus-fluctuations of this inhibitor pass the limit of visibility; (*b*) that there are two factors, *A* and *B*, which have no visible effect when existing alone, but which act as an inhibitor when brought together. These two hypotheses must be tested by further breeding.

I take pleasure in acknowledging here the faithful work of Mr. E. E. BARKER, who assisted me in making the records upon which this paper is based.

STATION FOR EXPERIMENTAL EVOLUTION
COLD SPRING HARBOR, L.I.

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CONTRIBUTIONS FROM THE ROCKY MOUNTAIN HERBARIUM. XI

NEW PLANTS FROM IDAHO

AVEN NELSON

(WITH TWO FIGURES)

The papers in this series numbered IX and X both dealt with novelties secured by Mr. J. FRANCIS MACBRIDE, of New Plymouth, Idaho, in his collections of 1910. The region that proved of greatest interest during that season was certain portions of Owyhee County in the southwestern part of the state. However, he found it possible to visit other counties, and in all of them much of interest was secured.

He spent the season of 1911 also in the field, revisiting some of the favored localities at earlier dates, and going into new fields later in the season. The writer found it possible to join MACBRIDE in his work during the month of July, at which time certain of the lava lands of southern Idaho were investigated. A few days were spent also in the Sawtooth and in the Lemhi National forests. This and a succeeding paper will deal with some of the many interesting things that were found. The plants to be sent out will bear MACBRIDE'S numbers, but those secured while both were in the field will have both collectors' names upon the labels.

Sisyrinchium inalatum, n. sp.—Roots coarsely fibrous, inordinately numerous from the small cormlike rhizome, widely spreading: stems simple, tufted and crowded, erect, 3–4 dm. high, rather stout, wholly wingless, leafy below, more than twice as long as the longest leaf, about 10-striate: leaves 9–15-nerved, hyaline-margined at the middle only where they are often 6–8 mm. broad, the upper half somewhat divergent, either straight or somewhat arcuate: the outer spathe large and conspicuous, 4–6 cm. long, many-nerved, at its widest part (where it is more or less scarious-margined) 8–10 mm. broad, tapering gradually to the apex, usually surpassing even the mature umbel by nearly half (sometimes more),

the upper one-fourth closed: inner spathe 6–8-nerved, with intermediate nerves, the whole margin broadly hyaline, less than half as long as the outer and shorter than the mature pedicels: scales thin, silvery scarious, from half to nearly as long as the inner spathe, the primary one with 3 conspicuous green nerves: flowers 1–4, medium size, seemingly purple or purplish (the material at hand quite mature and the flowers out of condition): stamineal column short: pedicels erect, 25–45 mm. long: capsules 5–6 mm. long, obovoid-globose but evidently trigonous, pale green: seeds about 15, 2 mm. long, flattened-oval, sometimes slightly trigonous or rhomboidal but always compressed and more or less wing-margined, and rugulose-pitted.

It is not clear to what species this is most nearly allied, but it is so strongly marked by its mass of fibrous roots, its stout wingless stems, its broad leaves and spathes, and its large capsule and numerous large winged seeds, that its recognition is not difficult.

MACBRIDE's no. 909, Silver City, June 17, 1911, is the only collection at hand. This, singularly enough, was secured on a dry open hillside.

Eriogonum shoshonensis, n. sp.—Annual, 1–2 dm. high, more or less white-lanate throughout and densely so on the under side of the leaves: stems few to several from the base, slender, dichotomously or tricotomously branched, the lower internode rather long, the succeeding ones gradually shorter, all the branches rather closely erect and therefore appearing fasciculately crowded above: leaves open-rosulate, 1–2 cm. long, on slender petioles as long or longer: bracts minute, triangular-subulate: involucres sessile, in the forks and lateral, and rather numerous on the branchlets, firm and somewhat angled by the thickened greenish nerves that terminate in the very short teeth, nearly tubular, about 2 mm. long, 5–10-flowered: perianth glabrous, on slender unjointed filiform pedicels which protrude about 1 mm.; perianth segments pinkish-white, with greenish midrib, obovate, obtuse, 2 mm. long, the outer noticeably broader than the inner: achene ovoid-triangular, abruptly contracted into a rather slender beak, nearly as long as the body, both together as long as the perianth.

Probably most nearly allied to *E. truncatum* T. & G. Proc. Amer. Acad. 8:173, but differing essentially in habit. That may perhaps best be described

as stemless, with a short stout peduncle from the summit of which spring few–several foliar-bracted rays which are then dichotomous or trichotomous. The involucre of that species is tubular campanulate.

Secured by NELSON and MACBRIDE at Shoshone, Idaho, in the rich lava soil of sagebrush swales, July 18, no. 1186.

Polygonum emaciatum, n. sp.—Very slender glabrous silver-green annual, 15–40 cm. high: stem usually simple below but branching dichotomously from near the base and upward, the internodes rather long, noticeably geniculate at the nodes so as to give the stems and branches a zigzag aspect: leaves few, linear, revolute, short, or even reduced to mere bracts: sheaths scarious, irregularly lacerate into a few acuminate awns: flowers in slender, rather open, terminal, spicate racemes; 1 or 2 in the axils of the small bracts which are more or less concealed by the lacerate sheaths; pedicels short, slender, erect, not exserted: perianth segments obovate-cuneate, whitish with a red line, about 3 mm. long: ovary oblong, triangular, as long as the slender styles: mature fruit not at hand.

This suggests *P. tenue* Michx., from which its peculiar skeletonized appearance, its zigzag branching, its very small not cuspidate leaves, and its usually solitary white flowers easily separate it.

The type is MACBRIDE'S no. 1692, "doby" lava slopes, near Sweet, Idaho, August 14, 1911; also by JUNE CLARK, August 18, no. 269, in the same locality.

Loeflingia verna, n. sp.—A diminutive, vernal, glabrous annual, 1–5 cm. high, with short filiform root: stem simple or with few-several filiform ascending branches: leaves triangular-subulate, not cuspidate, 2 mm. or less long, opposite at the few nodes: flowers few, solitary-axillary on rather long filiform pedicels forming an open few-flowered cyme: sepals 5, entire, about 3 mm. long, lanceolate, acute, scarious-margined, 1-nerved but neither carinate nor setaceous tipped: petals usually wanting, if present scarious, narrowly lanceolate, as long as the sepals, apparently 3 only: stamens 3 or rarely 5: anthers small, on capillary filaments, stigmas 3 (or 2?), subsessile but distinct: ovary several-ovuled; capsule 1-celled, ovoid-triangular, as long as the sepals: seeds attached to the central-basal placenta on rather long funiculi: embryo moderately curved, accumbent.

It is interesting to add another American species to this singularly erratic genus. I have no doubt that the describer of *L. pusilla* Curran was right in her observation "stamens 5," in spite of the fact that later observers have noted only 3. The plants now at hand show this tendency to vary the number of stamens, and occasionally to develop petals also. Is the following statement of the manuals correct, "ovules attached laterally," or does the wording in this description come closer to the fact?

Secured by MACBRIDE in the grass among the sagebrush, on the plains near New Plymouth, April 24, 1911, no. 773.

ARABIS LIGNIPES **impar,** n. var.—Larger and coarser than the species (*A. lignipes* A. Nels. BOT. GAZ. **30**:191. 1900), the lignescent caudex apparently more enduring, often 8–10 cm. high and marked only by the scalelike leaf bases: pubescence extending to the inflorescence and mature pods.

The type of this variety is MACBRIDE'S no. 828, dry, stony slopes, on Squaw Creek, Sweet, Idaho, May 8, 1911. I refer here also specimens by C. N. WOODS, Hailey, Idaho, no. 9*a*, 1910.

DRABA LAPILUTEA A. Nels. in Coult. & Nels. Man. 222. 1909. *D. yellowstonensis* A. Nels. BOT. GAZ. **30**:189. 1900.—Fine specimens of this strongly marked species were secured by NELSON and MACBRIDE on a high mountain near Mackay. It accords very closely with the type except that some of the specimens indicate that it may sometimes at least be perennial. The flowers are truly white and not merely so on fading.

Draba McCallae and *D. columbiana* Rydb., Bull. Torr. Bot. Club **29**:241. 1901, are very near allies, if indeed they be not both referable to *D. lapilutea*.

Parrya Huddelliana, n. sp.—Perennial from very long slender flexible woody roots which penetrate far down among the rocks in subalpine slides: caudex of few–several very slender (almost filiform) somewhat scaly branches which elongate (even to several dm.) sufficiently to bring the herbage out among the surface rocks: leaves rosulate on the tips of the branches of the caudex, with some scales or petioles for a few cm. below, narrowly spatulate-oblanceolate, 12–25 mm. long, somewhat cinereous with a stellately branched pubescence: inflorescence a short crowded corymbose raceme almost hidden among the leaves but the pedicels elongating in fruit, the few–several large pods appearing umbellate upon rays 10–15 mm. long: pods oblong or bicuneate, 2–3 cm. long, the acute

apex tipped with the short, slender, obscurely lobed stigma, very flat, with perfect septum and the few large seeds in two rows: seeds oval, silvery-white, with a crisped or cellular seed-coat.

To find so perfect an example of a true *Parrya* in this region was a most agreeable surprise. It is nearer to *P. arctica* R. Br. than to *P. macrocarpa* R. Br.

This fine species was discovered by COLUMBUS I. HUDDLE, supervisor of the Lemhi National Forest, Mackay, Idaho. It was growing in the loose black-limestone slide-rock, in Bear Canyon, altitude about 10,000 feet. The specimens, secured in good quantity, were in full fruit. The species is named for its discoverer, to whose courtesy the writer owes the memory of a glorious summer day's splendid collecting in the forest, under Mr. HUDDLE'S watchful supervision, July 30, 1911. Distributed under NELSON and MACBRIDE'S no. 1466.

CHYLISMA SCAPOIDEA **seorsa,** n. var.—Annual or winter annual, green and glabrous in appearance but minutely puberulent on stems and in the inflorescence: stems branching from the base and upward, 2–3 dm. high, equally leafy up to the rather long naked open raceme, the basal leaves falling away sooner than the upper: leaves oblong to ovate or even obovate, entire or denticulate with callous-tipped teeth.

The best example of this at hand is AVEN NELSON'S no. 4125, Evanston, Wyo., July 27, 1897. NELSON and MACBRIDE'S no. 1145, King Hill, July 16, 1911, is also referable to this variety.

Taraxia tikurana, n. sp.—Perennial from long, and in older plants, rather thick fleshy roots with 1–3 crowns, strictly acaulescent, green but under a lens sparsely and minutely appressed hirsutulous: leaves 8–15 cm. long (including the petiole), narrowly oblanceolate in outline, pinnately deeply and irregularly toothed, the rounded sinuses often extending to the midrib; the slender petiole shorter than the blade: flowers rather numerous, yellow; the calyx tube 6–10 cm. long, slender: calyx lobes narrowly lance-oblong, about 8 mm. long, twice as long as the obconic tube: petals large, obovate, emarginate or rounded, 10–14 mm. long: stamens unequal, the shorter stamens only about half as long as the others; anthers attached about one-third of their length from the base: capsule small, subulate, ridged by the rounded sutures; seeds in two rows, irregularly oblong.

This splendid species is nearest to *T. breviflora* Nutt., from which it is so different that there is no need to emphasize the differences.

MACBRIDE secured it in Jordan Valley, near Silver City, June 22, 1911; NELSON and MACBRIDE'S no. 1302, from Tikura, Blaine Co., is taken as the type. It seems to occur in the rich soil of river bottoms.

Cicuta cinicola, n. sp.—From a thick stout root (?)[1] widely and freely branched, 2 m. (more or less) high: leaves large; the lower often 1 m. long, bipinnate with some of the larger pinnae trifoliate, gradually reduced and simplified upward, the uppermost very small and trifoliate or simple; the leaflets of the lower leaves from ovate to broadly lanceolate, 12–20 cm. long including the long stout petioles, coarsely serrate, the teeth broadly triangular and abruptly apiculate; upward the leaflets become gradually smaller and narrower, the uppermost lance-linear and only 2–3 cm. long; involucre wanting or of a few green or rarely scarious-margined bracts, or sometimes a single foliar bract 2–4 cm. long: pedicels numerous, 3–7 mm. long; the involucels of many lance-linear, scarious-margined bractlets, as long as or longer than the pedicels: fruit strongly compressed laterally, the dorsal diameter twice as great as the lateral, about 3 mm. long, the stylopodium low-conical, the styles about 1 mm. long: the carpels somewhat oblique at base and more or less inequilateral: the low rounded ribs in surface display about equally the intervals in which lie the large irregular solitary oil tubes; commissural face plane, rather narrow, with two smaller oil tubes (fig. 1).

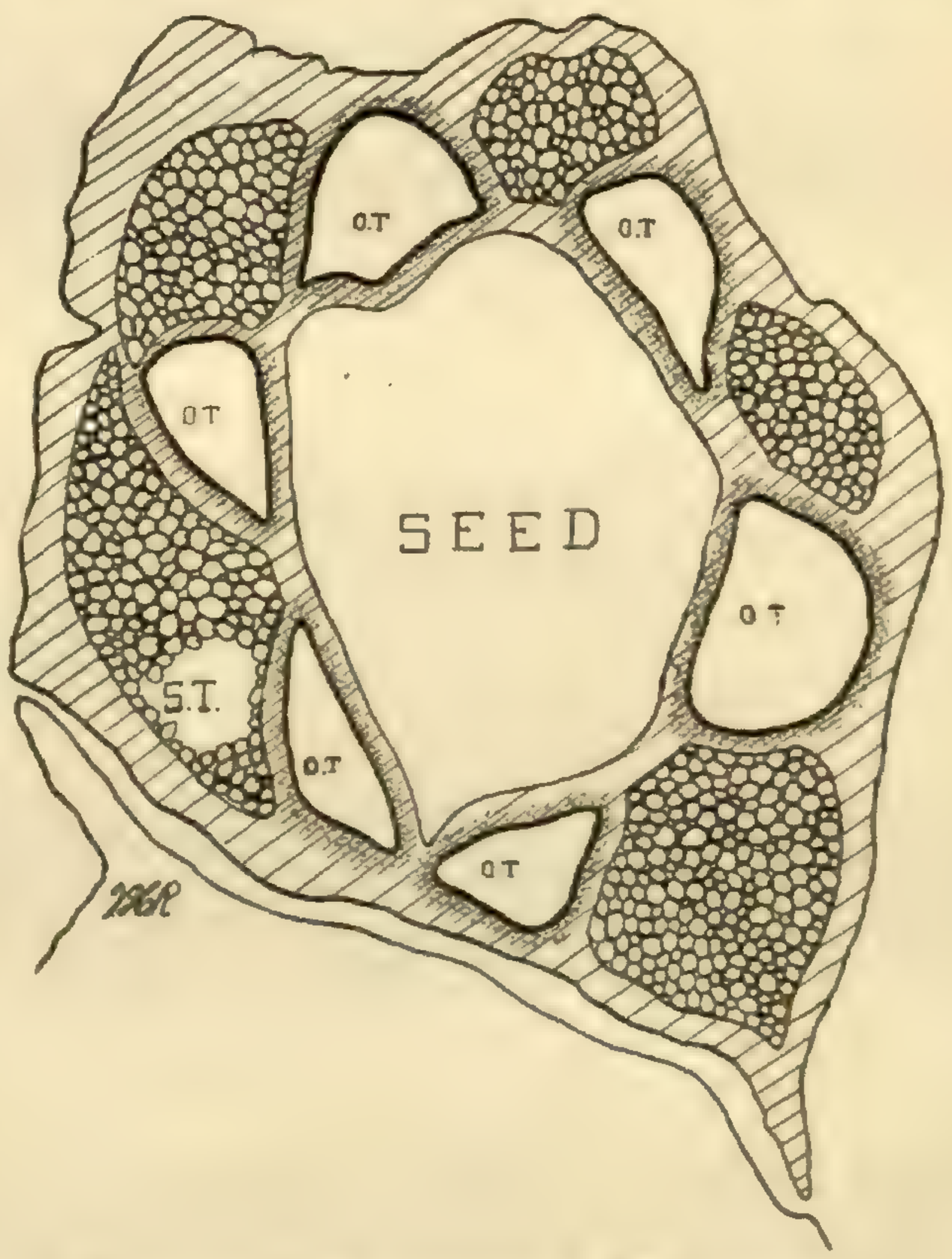

FIG. 1.—*Cicuta cinicola* A. Nels., n. sp.

[1] The root was not collected, but the impression of the collectors is that it was too large and deep-set to be removed with the means at hand.

This species is singularly like *C. Bolanderi* Wats., except for the much larger leaves and the large broad leaflets. The fruit, however, is much more flattened dorsally and the pericarp much thickened with strengthening tissue. It is extremely improbable, however, that the species heretofore supposed to be restricted to the tide-land marshes of Suisun, Cal., should next appear in the lava lands of Idaho.

The plants are large, stately, well branched, and conspicuous objects among the underbrush that borders Rock Creek, near Twin Falls. The stem at the base is often 4–5 cm. in diameter. The soil in this neighborhood is the well known volcanic ash that has proven so well suited to the production of apples. NELSON and MACBRIDE'S no. 1315, July 25, 1911, is the type.

Cynomarathrum Macbridei, n. sp.—Glabrous: acaulescent: root woody, surmounted by a branched caudex which is clothed

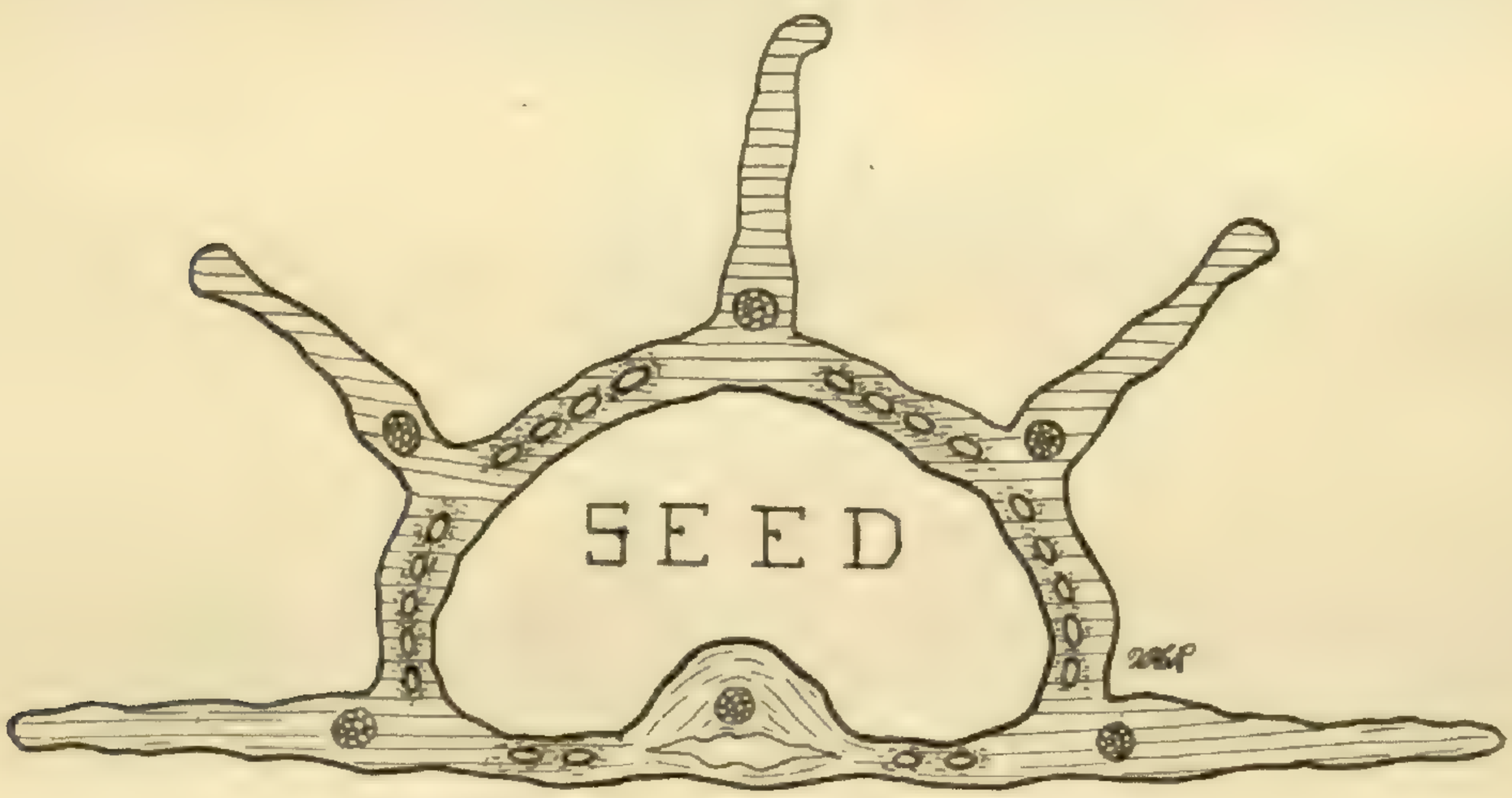

FIG. 2.—*Cynomarathrum Macbridei* A. Nels., n. sp.

with dead leaf bases: leaves narrowly oblong, bipinnate, 3–7 cm. long including the very slender petiole; the pinnae often pinnately cleft; the leaflets elliptic, very numerous and minute, only 1–2 mm. long: scapes 1–3 times as long as the leaves, slender: the flowers closely capitate in a small cluster, white: rays few and short (only a few mm.) even in fruit: pedicels nearly wanting: seeds flattened dorsally, all of the ribs thin-winged, the lateral more than half as broad as the body, the others not much narrower: oil tubes 3–5 in the intervals, 4–8 on the commissural side: calyx lobes evident: the stylopodium low and flat (fig 2).

This species is decidedly distinct from any of the known species in this genus. Some of its characters suggest the genus *Phellopterus*, but the char-

acteristic caudex and the presence of the stylopodium leave scarcely any doubt that it is a *Cynomarathrum*.

Secured by MACBRIDE in the shale slides near the summits of the mountains bordering Bear canyon, in the Lemhi National Forest, July 31, 1911, no. 1502.

DODECATHEON PAUCIFLORUM **shoshonensis,** n. var.—Similar to the species in size, but the root system consisting of a short corm from which the fleshy-fibrous roots seem to detach at the end of the season, at which time there has formed laterally on the corm 1 or 2 elongated bulblike buds. These probably give rise to the next year's plants. The flowers are paler than in the species.

The material at hand is rather scanty and over-mature. Possibly ampler collections may show further differences. The specimens were secured by NELSON and MACBRIDE at Shoshone Falls, July 26, 1911, no. 1362.

Phacelia firmomarginata, n. sp.—Annual or possibly biennial,[2] divaricately branched from the base, with assurgent branched stems 1–2 dm. long: pubescence short, fuscous, obscurely glandular, with some small scattering hispid hairs which are most numerous on the calyx: leaves alternate, rather small, 1–4 cm. long, sessile or short-petioled, oblong in outline, pinnately cleft or parted into few ovate or obovate crenulate-toothed lobes: the ebracteate spikes dense even in fruit, 3–6 cm. long: calyx decidedly enlarged in fruit, apparently persistent, cleft to the base and only loosely inclosing mature capsule; sepals narrowly oblong-lanceolate, at maturity about 1 cm. long, reticulated by the veins which run from the stout mibrib to the greatly thickened firm hispid margins: corolla minute, pale or white, much shorter than the calyx, the rounded denticulate lobes about half as long as the short broad tube, the vertical folds obsolete; stamens and style well included: capsule ovoid, minutely hispid-pubescent, 3–4 cm. long, 4-seeded: seeds oblong, about 2 mm. long, brown, distinctly pitted.

Probably nearest *P. hispida*, from which it is quite distinct. It is a plant of the desert, being secured by MACBRIDE on dry hillsides near Twilight Gulch in Owyhee County, June 23, 1911, no. 979.

PHLOX LONGIFOLIA **filifolia,** n. var.—The woody caudex short, freely branched: the stems delicately filiform, 1–3 dm. long: leaves filiform, about 1 mm. broad, mostly 3–6 cm. long but often

[2] In full fruit June 23 and the root leaves largely wanting.

longer: bracts, pedicels, and calyx glandular-pubescent: corolla tube one-half longer to nearly twice as long as the calyx lobes.

The strongest character of the variety is its glandular inflorescence and its longer corolla tube. Represented by NELSON and MACBRIDE'S no. 1192 from Ketchum, July 19, 1911, found among the sagebrush on the river bottom lands.

Gilia Burleyana, n. sp.—Perennial from a completely lignified, rather large root, with a more or less branched caudex, producing few–many slender leafy suberect stems, 15–30 cm. high: pubescence scanty, soft and crisped, more abundant on stems and inflorescence than on the leaves: leaves alternate, small, numerous, entire, linear, 1-nerved, slightly thickened on the margins, mucronate-tipped, 1–4 cm. long: inflorescence capitate, or of 2 or more heads in a terminal congested corymb: flowers numerous, small and very crowded: calyx tube delicately scarious, twice as long as the greenish hirsute subulate mucronate lobes: corolla white, tubular, with more or less reflexed lobes half as long as the tube; tube less than 5 mm. long, slightly exceeding the calyx, obscurely pubescent within: anthers exserted; filaments inserted in the sinuses, shorter than the corolla lobes: style about equalling the stamens: ovules solitary in the cells, usually only one maturing and producing an inequilaterally distended capsule: seed large, oblong, slightly curved as is also the embryo, developing mucilage and spiracles when wetted.

This rather extraordinarily strong species falls into the section ELAPHOCERA Nutt. as arranged by Dr. BRAND in his recent monograph. Until now this section contained no perennials.

This species is named in honor of Mr. D. E. BURLEY, general passenger agent of the Oregon Short Line Railroad Company, whose cordial cooperation and intelligent interest in scientific work is so greatly appreciated. The type of the species is NELSON and MACBRIDE'S no. 1126, from loose white clay banks, a few miles from King Hill, Idaho, July 16, 1911.

Cryptanthe scoparia, n. sp.—About 15 cm. high, fastigiately branched from the base and upward, the erect branchlets broom-like in their compactness: pubescence of a few stiff hispid spreading hairs and a rather close layer of short white appressed ones: leaves linear, the hispid hairs from pustulate bases: racemes numerous, 3–6 cm. long at maturity: fruiting calyces numerous and rather crowded on the rachis: sepals very narrow, but thick, bluntly

subulate, 4–5 mm. long in fruit: corolla not seen: nutlets 4, about 2 mm. long, narrowly conical, attached their whole length by an open but narrow groove to a slender-subulate gynobase, the small areola at base scarcely forked, closely muricate with silvery-gray spinellae on a brown background.

Material in this genus is assigned with difficulty. Floral characters give but little clue. Aspect and the nutlets are the most reliable characters. Even these seem to vary much, but after making due allowance for this fact, the present specimens cannot be referred to *C. multicaulis* A. Nels., BOT. GAZ. **30**:194, nor to *C. grisea* Greene, Pitt. **5**:53, apparently the two nearest allies. Both of these differ essentially as to the nutlets.

The type is NELSON and MACBRIDE'S no. 1311, from sagebrush plains, near Minidoka, July 24, 1911.

PENTSTEMON CONFERTUS Dougl.—Perhaps in no group of *Pentstemon* does a tendency to vary with every change in the ecological conditions manifest itself so fully as in *P. confertus* and its allies. In this group there are three rather strongly marked species: *P. attenuatus*, *P. confertus*, and *P. procerus*, all by DOUGLAS. In recent years several others have been added, some as species and some merely as varieties. How many of these should stand may not yet be said, but certainly not all of them. The undue multiplication of species might be held measurably in check if we could reach some agreement as to the relative importance of the characters ordinarily relied upon in describing these plants. The diagnostic characters mostly used are (1) pubescence in corolla throat and on the sterile filament, (2) shape and size of the corolla and the calyx lobes, (3) glandulosity of the inflorescence, (4) pubescence on the herbage, (5) color of the corolla. Now it is evident that if one phytographer considers one of these as of fundamental value in determining relationship, and another takes one of the other characters as basic, and a third still another, and so on, the number of species that may be described by the rearrangement of these characters becomes merely a problem in permutation. It seems, therefore, that one ought to place first those characters which are probably modified the least by reason of a change of environment, that is, those characters which are fundamentally concerned with the perpetuation of the species should stand first and the others should be serially arranged in the order in which they

relate themselves to this one great fact of reproduction. To illustrate: in this *Pentstemon* group the characters enumerated above may well stand in the order given, for is it not probable that those points of structure concerned with insect visitation come true generation after generation, while such as viscosity, pubescence, and color may change with every change of environment?

How close are the three species enumerated may be seen in the following facts: all have the sterile filament and the lower lip of the corolla more or less bearded; all have the flowers in verticils (two or more); all have calyx lobes more or less scarious-margined and mostly more or less lacerate. If one undertakes to state categorically their differences, about all one can say even of supposedly typical material is:

1. *P. attenuatus*.—Flowers yellow, rather large (20 mm. or more); inflorescence glandular and pubescent.

2. *P. confertus*.—Flowers yellow but small (less than 20 mm. long); inflorescence pubescent or puberulent but not glandular.

3. *P. procerus*.—Flowers not yellow (usually blue-purple), small (less than 20 mm. long); inflorescence neither pubescent nor glandular.

Of the three species, no. 2 seems most readily maintained as a pure and fixed species. The scores of variants may rather satisfactorily be grouped under 1 and 3. This being true, why not let the large-flowered forms, having the other floral characters in harmony, constitute the variety?

P. attenuatus **varians,** n. var., without reference to color or the presence or absence of pubescence or glandulosity.

Similarly let the small-flowered variants, having the other floral characters of *P. procerus*, become *P. procerus* **aberrans, n. comb.**

This varietal name was used by M. E. JONES as *P. confertus aberrans*, but the specimens to which the name was applied are clearly of the *P. procerus* group (see Proc. Cal. Acad. **2**:5–715).

I am fully aware that this disposition of this troublesome group means the wrecking of several pseudo-species, among which may be named *P. micranthus* Nutt., *P. Owenii* and *P. Rydbergii* A. Nels., *P. pseudoprocerus* Rydb., and a score (more or less) of Dr. GREENE'S species (see vol. I of *Leaflets*).

As excellent examples of *P. attenuatus varians*, I name MACBRIDE'S no. 974,

Twilight Gulch, Owyhee County, June 23, 1911, and his no. 1693, Pinehurst, Boise County, August 17, 1911.

Pentstemon laxus, n. sp.—Minutely puberulent on stems and foliage, the pedicels and calyx wholly glabrous: stems solitary or few, from a compact mass of thick fibrous roots, slender and weak, 5–8 dm. high: leaves 6–9 pairs, not much reduced above, lanceolate-linear, 5–10 cm. long: flowers in a crowded subcapitate terminal cluster on a peduncle 6–12 cm. long and naked but for 1 or 2 pair of linear approximate bracts; besides the terminal cluster there are rarely produced from the axils of the upper leaves a pair of small pedicellate clusters: calyx short, cleft to the base; its lobes broadly obovate, obtuse, slightly erose, scarious with greenish center especially toward the tip, only 2–3 mm. long or about one-fifth as long as the corolla: corolla a vivid blue, narrowly tubular and only slightly dilated upward, 2-lipped, but the lips short, the longer lower lip densely bearded with long yellow hair; the lobes all very short, suborbicular: stamens glabrous, shorter than the corolla: sterile filament shorter than the fertile, not dilated, blue at tip, tapering and flexed at the very apex, glabrous or with 1–7 deciduous hairs.

This is probably not a very strong species, but it seems fully as distinct from any *Pentstemon* previously discussed as any two of them are from each other. Further, if made merely a variety it would be difficult to say to which one to unite it.

It was found on slopes in rich sagebrush lands. NELSON and MACBRIDE, no. 1196, Ketchum, July 19, 1911.

PENTSTEMON LINARIOIDES **seorsus,** n. var.—Very similar to P. linarioides Gray (Bot. Mex. Bound. 112), from which it differs primarily as follows:

Larger in every way, the rootstock notably woody: calyx green and only half as long as the corolla; its lobes ovate, abruptly acute, thick and green at tip, slightly scarious below: corolla glabrous in the throat: the sterile filament longer than the fertile ones and densely pubescent with short yellow hairs for its whole length.

At first it seemed impossible that these specimens from southwestern Idaho should be referable to a species so long known only from southern Colorado, New Mexico, and Arizona, and the above characters led to their being desig-

nated as a new species, *P. seorsus*. On further reflection it seems better, however, to consider them as representing merely a variety.

Collected by MACBRIDE at Twilight Gulch, Owyhee County, in lava fields, June 22, 1911, no. 970.

PENTSTEMON ERIANTHERA **Whitedii,** n. comb.—*P. Whitedii* Piper, BOT. GAZ. **22**:490. 1901.

Mr. PIPER, in Contrib. Nat. Herb. **11**: 500, reduces his species to a synonym of *P. erianthera* Pursh, but this was hardly justified. *P. erianthera Whitedii* is of different habit, producing several stems (instead of only 1 or 2) from a wood taproot; the stems are more slender; the leaves narrower and more numerous; the glandular-pubescence throughout is less pronounced; the sepals are lanceolate, acute (not acuminate); the corolla is light blue without any of the peculiar red found in typical *P. erianthera*. While the pubescence in the throat and on the sterile filament is of the same character, it is far less copious. For these reasons it seems that the northwest forms may well be carried as a variety of the typical Rocky Mountain *P. erianthera*.

NELSON and MACBRIDE'S no. 1421, secured at Mackay, on gravelly sagebrush slopes, July 30, 1911, is typical of the variety.

CASTILLEJA VISCIA Rydb.

The range of this excellent species is greatly extended by MACBRIDE'S no. 990 from Silver City, Owyhee County. While MACBRIDE'S plants are not quite typical, yet they help to a better understanding of the species. These are more densely glandular and lack the crimson or scarlet tips in bracts and corolla. The corolla is of the right proportions, but smaller.

Castilleja multisecta, n. sp.—Freely branched from a woody caudex, the ascending stems sparingly branched, 2–4 dm. high, including the long fruiting spike which is often more than one-third of the plant: pubescence inconspicuous, very softly lanate throughout: leaves 2–4 cm. long, numerous, pinnately parted into 5–7 narrowly linear lobes, the lateral ones sometimes again parted, the undivided base obcuneate and strongly 3-nerved: bracts resembling the leaves but the segments tipped with red, as are also the margins of the galea: calyx more deeply parted above than below, the primary lobes deeply toothed, the thin triangular teeth acute: corolla slender, about 3 cm. long; the galea being about one-third of this; the lower lip very short, saccate, its short broad truncate teeth with a central cusp: seeds beautifully honeycombed on the surface with shallow scarious cell walls.

In spite of the large number of species of *Castilleja* of somewhat similar aspects and with dissected leaves, I do not seem to be able to refer this to any near ally. The type number is NELSON and MACBRIDE'S 1261, secured on disintegrated granite slopes at Ketchum, Blaine County, Idaho, July 21, 1911.

MISCELLANEOUS SPECIES

Eriogonum loganum, n. sp.—Perennial with woody branched caudex, the current year's stems short, simple, leafy, densely white-lanate as are also the leaves, peduncles, and involucres, assurgent, 1 dm. or less long and terminating in a stout ascending scapelike peduncle 12–25 cm. high: leaves oblanceolate, mostly narrowly so, obtuse or subacute, very white and densely appressed lanate, 2–3 cm. long, on pedicels of about the same length: involucres tubular-campanulate, thin and scarious between the 5 or 6 nerves, 4–5 mm. long, many-flowered: perianth glabrous, pale (greenish-white), directly articulated to the capitate apex of the slightly exserted pedicels; perianth segments thin but with a stout rounded midrib raised on the inside, the outer and inner similar, oblong, obtuse, about 2 mm. long: achene glabrous, 3 mm. long, the ovoid-triangular body not longer than the tapering beak.

This description has been drawn from specimens supplied by CHARLES PIPER SMITH, of Logan, Utah, under no. 1704. It occurs on the dry bench lands or terraces near the college, and is in blossom late in June, with ripe achenes in July. These specimens have been referred to *E. ochrocephalum* Wats., but that species seems quite distinct from this.

LESQUERELLA LUNELLII **lutea,** n. var.—Much like the species, seemingly blossoming even the first year from seed, hence some specimens appear as annuals, some as biennials, and still others as perennials, with slender woody taproot: leaves narrowly oblanceolate: flowers yellow, a little larger than in the species.

This variety is probably only an ecological variation. Dr. LUNELL has now secured the species itself from several localities in Benson County, and these sustain the characters as originally given, including the purple blade of the petals. The variety he has secured in three other counties (Ward, McHenry, and Rolette), and it differs primarily in that the petals are yellow, as one expects them to be in this genus. It would no doubt have been more in harmony with our conception of the genus had the form with yellow petals been discovered and named first, the purple one becoming the variety.

Astragalus Batesii, n. sp.—Stems few to several, spreading from the summit of a slender woody taproot, only 1–4 cm. long, very leafy; leaves pinnate, 5–9 cm. long including the slender petiole; leaflets mostly 7–11, narrowly oblong, obtuse, strigose-canescent, greenish and becoming glabrate above: flowers in terminal, capitate, few–several-flowered racemes on very slender peduncles which in fruit equal or exceed the leaves; bracts lance-linear, silky, shorter than the silky calyx: calyx lobes linear, as long as the tube: corolla pale violet, 6–8 mm. long, exceeding the calyx, turning somewhat yellowish with age: pod strictly 1-celled, with straight keel except the tip, narrowly oblong, tapering to the acuminate or cuspidate tip, with short silky appressed pubescence, 12–15 mm. long, when mature lightly transverse rugose.

Rev. J. M. BATES, of Red Cloud, Neb., for many years a careful student of his local flora, contributes the fine specimens upon which this description is based. Having carefully studied the plant in the field and being familiar with the species of *Astragalus* of his range, he submitted this as probably different from any of the described species. In this opinion I must concur, and I therefore take this opportunity to dedicate the species to its discoverer. The species is most nearly allied to *A. lotiflorus* Hook. from which it is at once distinguished by its more appressed pubescence, its violet flowers, and its strictly 1-celled pod in which the dorsal suture is not at all impressed. The type is deposited in the Rocky Mountain Herbarium under the collector's no. 5501, Red Cloud, Neb., May 17 and May 23, 1911. A splendidly fruited specimen secured at the same place, June 9, 1909, in also deposited with the type.

Mertensia campanulata, n. sp.—Glabrous throughout, even to the calyx lobes: root thick and semi-fleshy, giving rise to few or solitary erect stems: stems moderately leafy, pale below: root leaves oblong, tapering to both ends, obtusish at apex, cuneate at base, the blade 8–12 cm. long, on petioles usually longer than the blade: stem leaves oblanceolate, tapering to a margined base, the middle ones the largest but these smaller than the root leaves, the uppermost very much reduced: panicle rather small and open, short-peduncled, 1–3 slender accessory peduncles from the uppermost leaves: calyx campanulate, about 5 mm. long, the broadly triangular obtusish lobes not more than one-fourth as long as the tube: corolla deep blue, beautifully veined with brown, 18–20 mm. long, tubular, the tube proper about half of it; the relatively long

throat but slightly dilated; the short lobes (3–4 mm.) abruptly reniformly expanded: anthers linear-oblong; filament inserted at the summit of the tube proper, as broad as the anther but only half as long, the two together as long as the throat: nutlets smooth or nearly so.

This seems to be an unusually strong species. Carelessly examined it might be referred to *M. ciliata*, but in reality it is closer to *M. Macdougallii* Rydb., of Arizona, from which it is clearly distinct and is equally distinct from *M. Leonardi* Rydb. Its calyx is distinctive in this genus.

Mr. C. N. Woods, supervisor of the Sawtooth National Forest, secured it "in moderately moist meadows" and sent in the ample specimens, at the same time calling attention to its salient characters. No. 325, Blaine County, Idaho, 1911.

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BENEFICIAL EFFECT OF CREATININE AND CREATINE ON GROWTH[1]

J. J. Skinner

(WITH ONE FIGURE)

This paper embodies a series of experiments on the influence of creatinine and creatine on seedling wheat. These experiments were made in an endeavor to throw light on the action of organic manures in soils, and the influence of soil organic matter on productivity. Creatinine has been discovered as a soil constituent in this laboratory by Dr. E. C. Shorey,[2] and an account of its occurrence and properties will be given elsewhere. This nitrogenous constituent occurs plentifully in animal products, wine, meat, etc., but has recently been found in these laboratories by Dr. M. X. Sullivan[3] to be a constituent part of many plants and seeds, and to occur in the medium in which plants have grown. The general methods for studying the effect of creatinine on plants in solution cultures is the same as that employed in connection with the harmful soil constituent, dihydroxystearic acid, previously reported in this journal.[4]

Effect of creatinine on growth

Two sets of cultures, composed of the fertilizer salts calcium acid phosphate, sodium nitrate, and potassium sulphate in varying proportions, used singly and in combinations of two and three, were prepared, the proportions varying in 10 per cent stages, thus making a total of 66 culture solutions according to the plan in the

[1] Published by permission of the Secretary of Agriculture, from the Laboratory of Soil Fertility Investigations.

[2] Shorey, Edmund C., The isolation of creatinine from soils. Jour. Amer. Chem. Soc. **34**:99. 1912.

[3] Sullivan, M. X., The origin of creatinine in soils. Jour. Amer. Chem. Soc. **33**:2035. 1911.

[4] Schreiner, O., and Skinner, J. J., Some effects of a harmful organic soil constituent. Bot. Gaz. **50**: 161. 1910; Ratio of phosphate, nitrate, and potassium on absorption and growth. Bot. Gaz. **50**: 1. 1910.

papers cited. Young wheat seedlings were grown in this series of solutions from March 3 to March 15. To one set of the 66 cultures only the nutrient salts were added, to the second set 50 ppm. of creatinine were added to each culture. Every three days the solutions were changed and analyzed.

When the two sets of cultures had grown for several days, it was noticeable that the creatinine plants were better developed, having broader leaves and longer and well developed roots. This was more noticeable in some of the fertilizer mixtures than in others.

The total growth made in the 66 cultures of nutrient salts without creatinine, designated as normal cultures, was 166.7 grams as against 181.2 grams in the case of the 66 cultures with 50 ppm. of creatinine. Putting the normal at 100, the latter becomes 109, or an increase of 9 per cent as an average of the 66 cultures. As already mentioned, the effect was much more pronounced in certain fertilizer combinations, especially those containing no nitrates, or those low in nitrates. The effects of creatinine in these cultures will now be considered in detail.

Effect of creatinine on growth in cultures containing no nitrate

Table I gives the growth of two sets of cultures composed of mixtures of phosphate and potash, varying in 10 per cent stages,

TABLE I

SHOWING THE EFFECT OF CREATININE ON GROWTH IN CULTURES CONTAINING NO NITRATES

No.	PPM. OF FERTILIZER INGREDIENT IN CULTURE SOLUTION			GREEN WEIGHT OF CULTURE IN GRAMS	
	P_2O_5	NH_3	K_2O	Without creatinine	With creatinine
1	0	0	80	1.400	1.576
2	8	0	72	1.470	2.200
3	16	0	64	1.950	2.100
4	24	0	56	1.527	2.000
5	32	0	48	1.490	2.200
6	40	0	40	1.558	2.408
7	48	0	32	1.795	2.328
8	56	0	24	1.540	2.400
9	64	0	16	1.444	2.220
10	72	0	8	1.400	2.100
11	80	0	0	1.100	1.150

there being no nitrate in the solutions; the concentration was 80 ppm. of $P_2O_5+K_2O$ in each culture. To one set of cultures was added 50 ppm. of creatinine. In the fifth column are given the green weights of the cultures without creatinine, and in the last column are given the weights of the cultures with creatinine. It is apparent from these figures that the creatinine has caused a

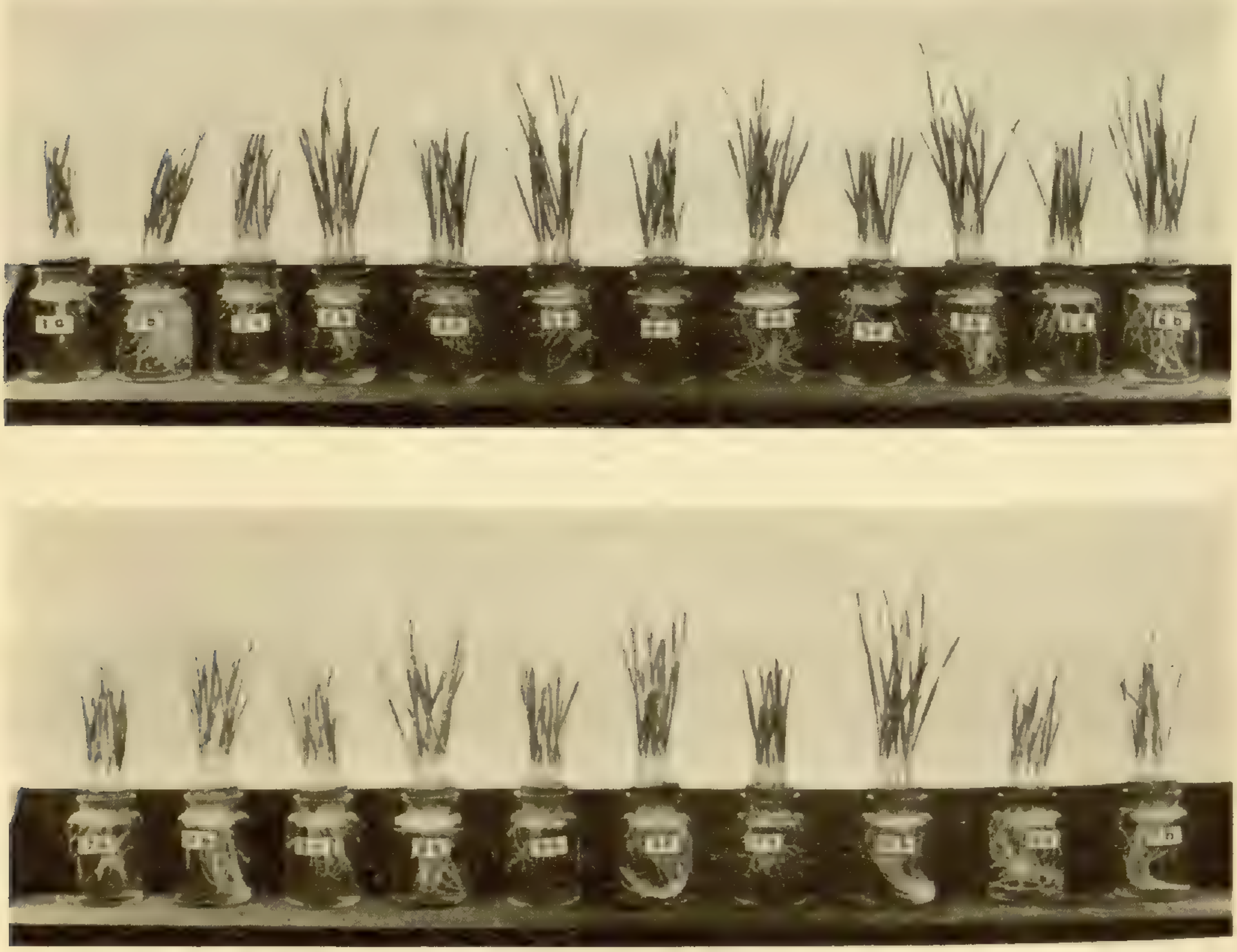

FIG. 1.—Wheat plants growing in culture solutions containing various proportions of potash and phosphate (with no nitrates) without (*a*) and with (*b*) creatinine.

considerable increase in growth. This is true in each of the 11 cultures. The total growth of the eleven cultures, without creatinine, was 16.674 grams against 22.682 grams for the cultures with creatinine. This is an increase of 36 per cent in the creatinine cultures.

The effect of creatinine in cultures with no nitrogen are shown in the plants in fig. 1. Cultures marked with the same number, for instance 1*a* and 1*b*, have similar fertilizer ratios. The cultures marked *a* have no creatinine, the numbers with the letter *b* have

50 ppm. of creatinine. As shown in the photograph, the plants in each culture containing creatinine, regardless of the proportion of potash and phosphate, is larger than the plants grown in a similar solution without the creatinine. The increased growth is noticeable in the roots as well as the tops. The tops in each case are broader and taller, the roots are larger and better branched.

Effect of creatinine in cultures containing 8 ppm. NH_3 as nitrate

Since creatinine was very beneficial in cultures containing no nitrate, it is interesting to observe its effect in cultures which contain a small amount of nitrate. Table II gives the result of the

TABLE II

SHOWING THE EFFECT OF CREATININE ON GROWTH IN CULTURE SOLUTIONS COMPOSED OF FERTILIZER MIXTURES, CONTAINING 8 PPM. OF NH_3 AS NITRATE

No.	PPM. OF FERTILIZER INGREDIENTS IN CULTURE SOLUTION			GREEN WEIGHT OF CULTURE IN GRAMS	
	P_2O_5	NH_3	K_2O	Without creatinine	With creatinine
1	0	8	72	1.820	2.190
2	8	8	64	2.470	3.100
3	16	8	56	2.748	3.250
4	24	8	48	2.907	3.420
5	32	8	40	2.670	2.450
6	40	8	32	2.928	3.258
7	48	8	24	2.526	3.340
8	56	8	16	2.600	3.000
9	64	8	8	2.048	2.359
10	72	8	0	1.354	1.750

effect of creatinine on growth in culture solutions composed of 8 ppm. of NH_3 as nitrate, and varying amounts of phosphate and potash, the total concentration of each solution being 80 ppm. of $P_2O_5+NH_3+K_2O$. By comparing the figures it is seen that the growth with creatinine, given in the last column, is larger than the growth without creatinine, given in the fifth column. The difference, however, is not nearly so large as in solutions containing no nitrate, presented in table I. The total green weight of the cultures composed of fertilizer mixtures containing 8 ppm. of nitrogen without creatinine was 24.071 grams against 28.117 grams in the cul-

tures with creatinine, an increase of 17 per cent. In the cultures with no nitrate creatinine produced an increase of 36 per cent.

Effect of creatinine in cultures with larger amounts of nitrate

It has been shown that creatinine was very beneficial in cultures which contained no nitrates. In a group of cultures, composed of mixtures of phosphate and potash in different proportions, creatinine increased the growth 36 per cent. It has also been pointed out that the beneficial effect of creatinine was not so great in cultures containing a small amount of nitrate. In a second group of cultures, composed of mixtures of potash, phosphate, and 8 ppm. of NH_3 as nitrate, creatinine increased the growth only 17 per cent.

In table III are given the results of growth in cultures with and without creatinine, composed of mixtures of phosphate, potash, and nitrogen having 16 ppm. NH_3 as nitrate. The green weights of the creatinine cultures given in the last column of the table are slightly larger than the normal cultures, as shown in the fifth column. The total green weight of the cultures without creatinine was 25.516 grams against 27.573 grams for the cultures with creatinine, an increase of 8 per cent.

TABLE III

SHOWING THE EFFECT OF CREATININE IN CULTURES CONTAINING 16 PPM. OF NH_3 AS NITRATE

No.	PPM. OF FERTILIZER INGREDIENTS IN CULTURE SOLUTION			GREEN WEIGHT OF CULTURES IN GRAMS	
	P_2O_5	NH_3	K_2O	Without creatinine	With creatinine
1	0	16	64	2.200	2.570
2	8	16	56	3.200	3.720
3	16	16	48	3.500	3.500
4	24	16	40	3.097	3.702
5	32	16	32	3.250	3.250
6	40	16	24	3.228	3.300
7	48	16	16	2.975	3.240
8	56	16	8	2.626	2.551
9	64	16	0	1.440	1.740

In other cultures composed of the three fertilizer ingredients P_2O_5, NH_3, and K_2O, but containing 24 ppm. of NH_3 as nitrate, creatinine increased growth only 2 per cent. Its effect in cultures

composed of fertilizer mixtures having more than 24 ppm. of nitrate was uncertain; in some cases there was a slight increase in growth and in others there was a slight decrease, that is, the growth with these higher amounts of nitrate in the solution was practically the same in the normal and creatinine cultures.

Before discussing further the effect of creatinine, it will be necessary to recall the effect which nitrates have on the growth of plants in mixtures of the other two fertilizer ingredients potash and phosphate. In work previously published,[5] it was shown that the better growth occurred in the normal cultures when the three fertilizer elements P_2O_5, NH_3, and K_2O were present. It was best in mixtures which contained approximately equal amounts of NH_3 and K_2O and a small amount of P_2O_5 (about 16 ppm.). The growth in the cultures containing the three constituents was much greater than in the cultures containing only two constituents. This was especially marked when nitrogen was not in the composition. In illustration of this, the average growth of a number of cultures, composed of mixtures of phosphate and potash in amounts of 80 ppm. of $P_2O_5+K_2O$, was 1.000 gram against 3.155 grams as the average growth of cultures composed of mixtures of these two ingredients, with an addition of only 8 ppm. of NH_3 as nitrate, the total concentration of nutrients being the same. In a second experiment conducted in a similar manner, but at a later date, the average growth of the cultures, composed of mixtures of phosphate and potash, was 0.878 gram, and the average growth of cultures, in mixtures of the three ingredients, containing 8 ppm. of NH_3 as nitrate, was 2.107 grams.

In the present experiment the growth in the normal cultures composed of varying proportions of phosphate and potash, compared with the growth in mixtures of these two ingredients, with 8 ppm. of NH_3 as nitrate added, is given in table IV. By a close examination of the figures in this table, it is seen that the growth in the mixtures of phosphate and potash is smaller than in cultures composed of mixtures of the three ingredients, though containing

[5] SCHREINER, O., and SKINNER, J. J., Ratio of phosphate, nitrate, and potassium on absorption and growth. BOT. GAZ. **50**: 1. 1910. Some effects of a harmful organic soil constituent. Bull. 70, Bureau of Soils, U. S. Dept. Agric. 1910.

but 8 ppm. of NH_3. The average growth of the cultures without nitrogen is 1.516 grams against 2.407 grams with 8 ppm. of NH_3 in the fertilizer mixture. Putting the growth of the cultures without nitrogen at 100, the relative growth of the cultures with nitrogen becomes 159, or an increase of 59 per cent.

TABLE IV

SHOWING THE GROWTH OF CULTURES, COMPOSED OF FERTILIZER MIXTURES CONTAINING NO NITRATE, AND 8 PPM. OF NH_3 AS NITRATE, WITHOUT AND WITH CREATININE

No.	PPM. OF FERTILIZER INGREDIENTS IN CULTURE SOLUTION			GREEN WEIGHT OF CULTURES IN GRAMS			
				Without creatinine		With creatinine	
	P_2O_5	NH_3	K_2O	No nitrate	8 ppm. NH_3	No nitrate	8 ppm. NH_3
1.....	0	0	80	1.400	.....	1.576	.....
2.....	0	8	72	.....	1.820	.....	2.190
3.....	8	0	72	1.470	.....	2.200	.....
4.....	8	8	64	.....	2.470	.....	3.100
5.....	16	0	64	1.950	.....	2.100	.....
6.....	16	8	56	.....	2.748	.....	3.250
7.....	24	0	56	1.527	.....	2.000	.....
8.....	24	8	48	.....	2.907	.....	3.420
9.....	32	0	48	1.490	.....	2.200	.....
10.....	32	8	40	.....	2.670	.....	2.450
11.....	40	0	40	1.558	.....	2.408	.....
12.....	40	8	32	.....	2.928	.....	3.258
13.....	48	0	32	1.795	.....	2.328	.....
14.....	48	8	24	.....	2.526	.....	3.340
15.....	56	0	24	1.540	.....	2.400	.....
16.....	56	8	16	.....	2.600	.....	3.000
17.....	64	0	16	1.444	.....	2.220	.....
18.....	64	8	8	.....	2.048	.....	2.359
19.....	72	0	8	1.400	.....	2.100	.....
20.....	72	8	0	.....	1.354	.....	1.750
21.....	80	0	0	1.100	.....	1.150	.....

With 50 ppm. of creatinine in the solution, the cultures containing no nitrogen produced better growth than the corresponding cultures without creatinine, as shown in the last two columns of table IV. The difference between the last two columns is not as marked in the creatinine set as in the corresponding columns for the normal set. The average growth of the creatinine cultures without nitrate is 2.062 grams against 2.812 grams for the cultures having 8 ppm. of NH_3 as nitrate in the fertilizer mixture. If the growth of the cultures without nitrate is put at 100, the growth with 8 ppm.

of NH_3 in the fertilizer mixture becomes 136, or an increase of only 36 per cent. In other words, in the absence of creatinine from the cultures, the nitrate (8 ppm.) caused an average increase of 59 per cent in the various cultures; in the presence of the creatinine (50 ppm.) the nitrate (8 ppm.) caused an average increase of only 36 per cent. It appears, therefore, that plants supplied with creatinine do not respond so markedly to added nitrate, thus seeming to indicate that the plant can utilize this nitrogenous compound for plant syntheses.

Effect of creatinine on absorption of fertilizer salts

The foregoing discussion has shown clearly the influence of creatinine on growth and its effect in cultures containing no nitrates. There remains to be discussed the effect of the creatinine on the removal of nutrients from the solution during the growth of the plant.

Mention has been made already of the fact that the concentration differences produced by the growth of the plants in the various cultures were determined by making an analysis for nitrates at the termination of every three-day change, and of the phosphates and potassium on a composite of the solutions from the four changes. It is thus possible to compare the results obtained under the so-called normal conditions without the creatinine and under the conditions where 50 ppm. of creatinine were present in the solution.

The sum total of P_2O_5, NH_3, and K_2O removed from solution by the growing plants in the cultures containing all three of these constituents was 1684 milligrams under the normal conditions, and 1584 milligrams in the creatinine set. The figures show the total of plant nutrients to be slightly less in the creatinine set, although the green weight in this set was 9 per cent greater than in the normal set. The examination of the results for the three constituents separately as given below shows that the phosphate and potash were slightly greater than normal, as is demanded by the larger growth, whereas the nitrate is considerably less than in the normal set.

Phosphate.—The amount of phosphate stated as P_2O_5 removed from the total number of solutions during the experiment was 364 milligrams for the normal cultures and 383 milligrams for the cul-

tures containing creatinine, a difference of 19 milligrams in favor of the creatinine cultures.

Potassium.—The amount of potash stated as K_2O removed by the plants in the total number of cultures was 760 milligrams in the case of the normal cultures and 778 milligrams for the cultures with creatinine. As with the phosphate, the creatinine cultures removed a little more potash than the normal cultures, there being a difference of 18 milligrams in favor of the creatinine set.

Nitrogen.—The total amount of nitrogen stated as NH_3 removed from the total number of solutions during the course of the experiment was 560 milligrams for the normal cultures and 423 milligrams for the creatinine cultures. The creatinine cultures though making a larger growth used 137 milligrams less nitrate.

Effect of creatine on growth

Creatine is closely related chemically to creatinine, the latter being the anhydride of creatine. Both probably occur in soils, manures, and green crops, a discussion of which is given in the two other papers referred to. Experiments in nutrient cultures with creatine have been conducted similar to those with creatinine.

The plants grew from April 22 to May 4. After the plants had grown for several days, it was apparent that the effect of creatine was very similar to that of creatinine. The leaves were broader, and further developed than those of the normal culture. The roots were longer and better branched. The plants growing in cultures with creatine, which contained phosphate and potash but no nitrate, were a great deal larger than similar cultures without creatine. Like the creatinine, when small amounts of nitrate were in the fertilizer mixture, the beneficial effect of creatine was not so marked, and in the presence of larger amounts of nitrate creatine had no additional effects.

The total green weight of 66 cultures containing the fertilizer salts only, that is the normal set, was 174.4 grams, against 186.8 grams for the 66 cultures containing 50 ppm. of creatine in addition to the fertilizer salts. This is an increase for the creatine cultures of 8 per cent over the normal cultures.

Table V shows the effect of creatine on growth in a number of

cultures containing varying amounts of phosphate and potash, but no nitrates, the amount of total fertilizer ingredient in each culture being 80 ppm. By an examination of the table it is apparent that the growth of each of the creatine cultures given in the last column is considerably larger than the growth of the cultures without creatine given in the fifth column. The total green weight of the cultures without creatine was 16.2 grams against 23.3 grams for the cultures with creatine, an increase of 44 per cent.

TABLE V

SHOWING THE EFFECT OF CREATINE ON GROWTH IN CULTURES CONTAINING NO NITRATE

No.	PPM. OF FERTILIZER INGREDIENT IN CULTURE SOLUTION			GREEN WEIGHT OF CULTURES IN GRAMS	
	P_2O_5	NH_3	K_2O	Without creatine	With creatine
1	0	0	80	1.329	1.709
2	8	0	72	1.420	1.948
3	16	0	64	1.558	2.130
4	24	0	56	1.579	2.370
5	32	0	48	1.528	2.470
6	40	0	40	1.500	2.400
7	48	0	32	1.670	2.270
8	56	0	24	1.628	2.420
9	64	0	16	1.600	2.450
10	72	0	8	1.428	2.070
11	80	0	0	0.978	1.090

In table VI are given the green weights of plants grown in cultures with and without creatine, containing 8 ppm. of NH_3 as nitrate and varying amounts of P_2O_5 and K_2O, the total constituents being 80 ppm. of $P_2O_5+NH_3+K_2O$. These figures show that the creatine cultures given in the last column are somewhat larger than the cultures without creatine given in the fifth column, but the difference is not nearly so large as in the cultures containing no nitrate given in table V. The total growth of the cultures without creatine was 26.4 grams against 29.4 grams for the cultures with creatine, an increase of only 11 per cent in favor of the creatine cultures. There was a difference of 44 per cent in favor of the creatine cultures in the case of the solution which contained no nitrate.

The growth in the cultures which contained varying amounts of phosphate and potash and 16 ppm. of nitrate was only 3 per cent greater with than without creatine. In solutions containing 24 ppm. of nitrate the increased growth with creatine was 6 per cent, and in solutions containing 32 ppm. nitrate the increased growth 4 per cent. In solutions containing higher amounts of nitrate the creatine had no additional effect. Thus it appears that the effect of creatine in replacing the effect of nitrate in producing growth is very similar to that of creatinine.

TABLE VI

SHOWING THE EFFECT OF CREATINE ON GROWTH IN CULTURES CONTAINING 8 PPM. OF NH_3 AS NITRATE

No.	PPM. OF FERTILIZER INGREDIENT IN CULTURE SOLUTION			GREEN WEIGHT OF CULTURES IN GRAMS	
	P_2O_5	NH_3	K_2O	Without creatine	With creatine
1	0	8	72	2.299	2.459
2	8	8	64	2.940	3.200
3	16	8	56	2.700	3.350
4	24	8	48	2.920	3.400
5	32	8	40	3.050	3.070
6	40	8	32	3.150	3.309
7	48	8	24	3.220	3.350
8	56	8	16	2.500	2.854
9	64	8	8	2.222	2.800
10	72	8	0	1.400	1.600

It is also interesting to note the effect of creatine on the removal of salts by the plants and the similarity between the action of creatine and creatinine in this respect. It will be remembered that in the creatinine cultures the removal of phosphate and potash was slightly greater in the creatinine cultures than the normal cultures, but a great deal less nitrate disappeared from solution in the creatinine than in the normal cultures.

In the creatine experiments the removal of total P_2O_5, NH_3, and K_2O by plants in the normal cultures was 1978.3 milligrams, against 1854.5 milligrams for the creatine cultures. The normal cultures removed 471.0 milligrams of P_2O_5 and the creatine cultures 474.4 milligrams. In the case of potash the normal cultures

removed 769.4 milligrams of K_2O against 767.4 milligrams for the creatine cultures. The removal of both phosphate and potash was practically the same in the normal and creatine cultures. The disappearance of nitrate was much less in the creatine than in the normal cultures. The normal cultures removed 737.7 milligrams against 612.7 milligrams for the creatine cultures, a difference of 125 milligrams.

The influence of the creatine in regard to the removal of P_2O_5, NH_3, and K_2O is very similar to that shown by creatinine, and it again appears that this substance as well as the creatinine can replace nitrates in its effect on plant growth.

BUREAU OF SOILS, U.S. DEPARTMENT OF AGRICULTURE
WASHINGTON, D.C.

BRIEFER ARTICLES

A NOTE ON THE GENERATIONS OF POLYSIPHONIA[1]

(WITH ONE FIGURE)

YAMANOUCHI[2] concludes from his cytological work on *Polysiphonia violacea* that "there is an alternation of a sexual plant (gametophyte) and an asexual plant (sporophyte) in the life history of *Polysiphonia*, the cystocarp being included as an early part of the sporophytic phase." He found that on the cystocarpic plants there was an occasional abnormality "in the form of a cell resembling a monospore, but having the same cell lineage as the tetraspore mother cell." He traced the development of these cells and found that although cleavage furrows appeared, the nucleus rarely entered a mitosis and the cell never divided. He makes note of the fact that LOTSY has found tetraspores on the same plants with sexual organs in *Chylocladia kaliformis* and that DAVIS has found the same condition in *Spermatothamnion Turneri*, *Ceramium rubrum*, and *Callithamnion Baileyi*. He suggests that possibly the structures reported as tetraspores are really monospores and are developed with a suppression of reduction phenomena, or that the sexual organs are developed apogamously.

LEWIS[3] has attempted an experimental test of the truth of YAMANOUCHI'S conclusion. He says: "Cytological observations on *Polysiphonia* by YAMANOUCHI, on *Griffithsia* by myself, and on *Delesseria* by SVEDELIUS render it probable that in these genera at least, and presumably in all Florideae in which tetraspores and sexual organs are borne on separate individuals, there exists an alternation of sexual and asexual plants, the carpospores giving rise on germination to asexual, and the tetraspores to sexual individuals." The results that he obtained by growing plants from the spores of *Polysiphonia violacea*, *Griffithsia Bornetiana*, and *Dasya elegans* are consistent with the above theory, no carpospores having been found to produce sexual individuals, and no tetraspores to produce asexual individuals. Both the cytological and the experimental evidence would thus seem to unite in indicating that

[1] Contributions from the Puget Sound Marine Station, no. 2.

[2] YAMANOUCHI, S., The life history of *Polysiphonia*. BOT. GAZ. **42**:401–449. 1906.

[3] LEWIS, I. F., Alternation of generations in certain Florideae. BOT. GAZ. **53**:236–242. 1912.

there is an alternation of generations in at least *Polysiphonia violacea*, and to offer at least some foundation for the belief that it is general among the red algae.

In 1911 Professor T. C. FRYE found in *Polysiphonia* material, collected at the Puget Sound Marine Station in 1910, some specimens showing both carpospores and tetraspores on the same individual. This observation was made in the course of laboratory work with a class and no material was kept. He suggested to the senior author of this note that the subject be investigated further at the Puget Sound Marine Station. The junior author examined the *Polysiphonia* material that was brought into the laboratory at the station during the session of 1911. In one lot of material she found the same condition to which Professor FRYE had referred. The material was collected in the lower littoral zone on the rocky shore of Turn Island, near Friday Harbor, Washington. It has been identified by Professor W. A. SETCHELL of the University of California as *Pterosiphonia bipinnata* and by Dr. SHIGÉO YAMANOUCHI of the University of Chicago as *Polysiphonia* sp.

FIG. 1.—Camera lucida drawing of a portion of a *Polysiphonia* (?), showing on the same individual both tetraspores and a cystocarp with a carpospore.

The fact that the mother cells had gone to the point of complete division into tetraspores in the material examined indicates that the tetraspores were not abortive, and the fact that carpospores were seen issuing from cystocarpic plants that bore also perfect tetraspores indicates that the cystocarps were not abortive. We have thus an individual that is both sexual and asexual, which is inconsistent with there always being in this species an alternation of a sexual individual and an asexual.

Professor T. C. FRYE and the senior author of this note are now at work on the cytology of specimens of this species with a view to determining the sporophytic or gametophytic nature of this generation by means of mitotic studies.—GEORGE B. RIGG and ANNIE D. DALGITY.

CURRENT LITERATURE

BOOK REVIEWS

Forest physiography[1]

This volume, intended primarily for the use of foresters, will be of very great value to ecologists, even to those working upon problems which are unrelated to forests. Its field of usefulness extends farther still, for it is the first work in which the much-scattered literature dealing with the physiography of various parts of the United States has been summarized and systematized. It will thus be frequently consulted by geologists, geographers, economists, and travelers. The ecologist as a rule must work out for himself the physiographic processes which are in immediate operation in his field of study. The value of Professor BOWMAN'S work will be found to lie principally along two lines: in the clearing up of the physiographic history of the region, and in comparison of the field of study with other parts of its physiographic region and with other regions.

The book comprises two parts. Part I is entitled "The soil," and is a summary of the present knowledge of that subject as it pertains to forest growth. This section is included because the influence of the physiographic processes upon forests is exerted largely through the formation, modification, and destruction of soils. It seems to the present writer that a better plan would have been to expand this section into a separate work, since the two parts of the book are essentially independent. The topics treated are as follows: importance, origin, and diversity of soils; physical features; water supply; temperature; chemical features; humus and nitrogen supply; soils of arid regions; soil classification.

In part II the physiography of the United States is considered by regions, each subdivision having "an essential uniformity or unity of geologic and physiographic conditions," and therefore a uniform topographic expression in the main. The sequence is from west to east. An introductory chapter discusses physiographic, climatic, and forest regions. In consideration of climate, full recognition is given to the combined effect of the various factors upon plant distribution, and yet MERRIAM'S "life zones" are accepted, although they are based upon temperature alone.

The chapters devoted to the various physiographic regions are largely descriptive of the present topography, with only such geologic details as are necessary to explain it. As the author remarks in the preface, the forester

[1] BOWMAN, ISAIAH, Forest physiography. pp. xxii+759. *pls. 6. figs. 292.* New York: John Wiley & Son, 1911.

is concerned with the relief of a region rather than with its geologic history. At the same time, the historical treatment is entirely adequate to satisfy the needs of an ecologist, and abundant references to the literature are given for the benefit of any who wish more detailed information. To illustrate the mode of treatment, the section devoted to the Adirondack Mountains may be cited. The subdivisions are as follows: geologic structure, topography and drainage, glacial effects, climate and forests.

The notes upon the forests which are appended to most of the sections are the least satisfactory portions of the work, being so brief and general as to be almost useless, and in one case at least inaccurate. The conifer forest of the southern Appalachian summits is referred to in three places. On p. 122 it is correctly described as "spruce and balsam." On p. 125 we read of the "spruce and hemlock forests on the summits of the Pisgah and other ranges in western North Carolina, where boreal conditions exist." The hemlock in these mountains is found principally in deep ravines in the lower hardwood forest belt, and rarely attains to the lower margin of the spruce-balsam forest. On p. 614 occurs the statement that "on the higher summits of the Great Smoky, Pisgah, and Balsam Mountains are a few thousand acres of black spruce," with no mention of the balsam, which is the more important of the two. On the same page, the author places the hemlock where it rightly belongs, in "shaded ravines and on the better watered northern or north-western slopes between 3000 and 5000 feet."

The book is adequately illustrated and has valuable physiographic and geologic maps. Its great weight is to be regretted, in a volume which one would wish to carry upon his travels.—WILLIAM S. COOPER.

A Yosemite flora

Professor and Mrs. H. M. HALL of the University of California are pioneers in the production of a local flora or handbook of one of our great natural playgrounds. Scores and scores of other local floras have been produced, but these have been as a rule mere check lists, and in all cases were intended to meet a local need. In this *Flora of the Yosemite*[2] we have a handbook that will find its largest use among strangers to the region. It is hardly necessary to call attention to the small size of this National Park as compared with the size of the great state of California, nor to the great size of the Park *botanically* considered. Within its 1024 square miles there are probably more kinds of soil and climate than can be found in any equal area in the world. This varied topography and climate have supplied the 955 species included in the flora. The grasses, sedges, and rushes are not included, but the authors conservatively estimate that these would swell the number to 1200, a number probably as great as that of an entire state in the prairie region.

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[2] HALL, HARVEY MONROE and CARLOTTA CASE, A Yosemite flora. San Francisco: Paul Elder & Co. $2.16.

The book possesses practically every feature that will contribute to its usefulness: an introduction to the Park itself; a chapter on the organography of the plant for those who have not had a course in botany; simple but complete keys; plain concise descriptions with a minimum of technical terms; interesting notes on habitat, habit, distribution, etc; 11 beautiful halftone plates in brown, and 174 instructive figures; a glossary and a complete index. This little manual of nearly 300 pages is significant in many ways. It indicates an increasing interest in technically correct science simply and clearly expressed. It emphasizes the fact that systematic botany should be developed for the *use* of the people, not to *impress* them with the futility of trying to fathom the mysteries of recent nomenclatural practices. It shows that the breeze is beginning to blow steadily from the ocean, littered with the wreckage of families, genera, and species, to the solid shores on which an *Astragalus* is an *Astragalus* and not a *Tium;* a *gentian* is a *gentian* and not an *Anthopogon;* and a *pine* is a *pine* and not an *apine*.

When a thing is so well done it seems almost ungenerous to mention matters which represent merely differences of opinion, but would it not have been well to have included the grasses, sedges, and rushes for the sake of completeness? Botanists would have valued this feature even if the descriptions had been very much curtailed. Attention may also be called to the seeming ultra-conservatism of the authors in the matters of the adoption of recent names for old, well known species. To a beginner, one technical name is as good as another, and no useful purpose is served by retaining a name that properly belongs in another range, even though that name has long been used in ours.

The publishers have done their work well. The binding is limp leather, the paper excellent in quality, and the pages are trimmed close, so that the little volume feels good in the hand and will no doubt find its way into the pockets of many of the visitors to the Yosemite Park.—AVEN NELSON.

NOTES FOR STUDENTS

Current taxonomic literature.—L. R. ABRAMS (Muhlenbergia **8**:26–44. 1912) gives a synoptical revision of the genus *Monardella*, as represented in southern California, and adds 4 new species, and 3 varieties.—O. AMES (Torreya **12**:11–13. 1912) has published a new *Habenaria* (*H. Brittonae*) from Cuba.—J. C. ARTHUR (Mycologia **4**:49–65. 1912) records the results of continued studies on the "Cultures of Uredineae in 1911."—O. BECCARI (Webbia **3**:131–165. 1910) under the title "Palmae australasiche nuove o poco note" has published several new species of palms and proposes a new genus (*Pritchardiopsis*) of this family from New Caledonia.—A. BRAND (Rep. Sp. Nov. **10**:280, 281. 1912) characterizes a new genus (*Namation*) of the Scrophulariaceae based on the Mexican plant *Nama glandulosum* Peter. The same author (*ibid.* 281) proposes the name *Andropus carnosus* for the plant hitherto doubt-

fully referred to the genus *Conanthus*.—N. L. Britton (Bull. Torr. Bot. Club **39**:1–14. 1912) under the title "Studies of West Indian plants IV" places on record important data and describes 20 new species of flowering plants.—The same author (Torreya **12**:30–32. 1912) adds a new species to the recently monographed genus *Hamelia*, namely *H. scabrida* from Jamaica.—N. L. Britton and J. N. Rose (*ibid.* 13–16) record 7 hitherto undescribed species of cacti from Cuba.—E. Chiovenda (Ann. Bot. **10**:25–29. 1912) under the title "Intorno a due nuovi generi di piante appartenenti alla famiglia delle Malpighiaceae" proposes two genera, namely *Tetraspis* and *Eriocaucantus*.—A. Cogniaux (Rep. Sp. Nov. **10**:343, 344. 1912) describes a new species of *Epidendrum* (*E. Rojasii*) from Paraguay.—L. Diels (Leafl. Phil. Bot. **4**:1161–1167. 1911) gives a synopsis of the Philippine Menispermaceae, recognizing 14 genera; the synopsis is based on a monograph of the group in the *Pflanzenreich* by the same author.—K. Domin (Rep. Sp. Nov. **10**:57–61, 117–120. 1911) describes several species of flowering plants from Australia and proposes a new genus (*Notochloe*) of the Gramineae.—A. D. E. Elmer (Leafl. Phil. Bot. **4**:1171–1474. 1911–1912) in continuation of his work on the Philippine flora has described upward of 150 new species of flowering plants.—A. Engler (Bot. Jahrb. **48**:224–336. 1912) in collaboration with several specialists has issued "Beiträge zur Flora von Afrika XL." About 120 species new to science are published, belonging mostly to the Solanaceae, Polygonaceae, and Umbelliferae. Four new genera of the Umbelliferae are proposed, namely *Afrosison*, *Marlothiella*, *Volkensiella*, and *Frommia*.—F. Fedde (Rep. Sp. Nov. **10**:311–315, 364, 365, 379, 380, 417–419. 1912), has published new species and varieties of *Corydalis* from North America.—M. L. Fernald and K. M. Wiegand (Rhodora **14**:35, 36. 1912) record a new variety of *Juncus* (*J. balticus* var. *melanogenus*) from Quebec.—C. N. Forbes (Occ. Papers Bern. Pau. Bish. Mus. Ethl. and Nat. Hist. **5**:1–12. 1912) under the title "New Hawaiian plants III" has published 4 new species of flowering plants.—E. L. Greene (Leafl. Bot. Obs. and Crit. **2**:165–228. 1912) has described about 100 new species of North American flowering plants mostly referred to *Apocynum* and *Erigeron*.—D. Griffiths (Rep. Mo. Bot. Gard. **22**:25–36. *pls. 1–17*. 1911) in a fourth article on *Opuntia* has described and illustrated 10 new species from southwestern United States and Mexico.—W. B. Grove (Journ. Bot. **50**:9–18, 44–55. *pls. 515, 516*. 1912) in an article entitled "New or noteworthy Fungi, part IV" includes the description of a new genus (*Cryptostictella*) found on leaves of *Tilia europea* at Studley Castle, England.—The same author (*ibid.* 89–92) has proposed the generic name *Diplosphaerella*, to include the species which have 16 spores in the ascus; the genus is based on *Mycosphaerella polyspora* Johans.—E. Hackel (Rep. Sp. Nov. **10**:165–174. 1911) under the title "Gramineae novae VIII" describes several new species of grasses including 9 from Mexico and South America.—E. Hassler (*ibid.*, 344–348. 1912) has published new species and varieties in the Rutaceae, Simarubaceae, and Scrophulariaceae from Paraguay.

—A. A. HELLER (Muhlenbergia **7**:125–132. 1912) describes and figures a new species of *Ivesia* (*I. halophila*) from the Ruby Mountains, Nevada; and (*ibid.* **8**:21–24. *pl. 4*) records a new *Apocynum* (*A. cinereum*) from the same state.—G. HIERONYMUS (Rep. Sp. Nov. **10**:41–53, 97–116. 1911) has published 19 new species of *Selaginella* from the Philippine Islands.—P. B. KENNEDY (Muhlenbergia **7**:133–136. 1912) describes a new willow (*Salix caespitosa*) from Mt. Rose, Nevada.—F. D. KERN (Torreya **11**:211–214. 1911) records 2 new species of *Uromyces* from the Central and Southern States.—F. KRÄNZLIN (K. Sv. Vet. Akad. Handl. **46**: no. 10. 1–105. *pls. 1–13.* 1911) under the title "Beiträge zur Orchideenflora Südamerikas" has published 78 new species of orchids, mostly from Brazil. The descriptions are supplemented by illustrations bringing out the more salient floral characters.—G. KÜKENTHAL (Leafl. Phil. Bot. **4**:1169–1170. 1911) records a new *Carex* (*C. palawanensis*) from the Philippine Islands.—H. LÉVEILLÉ (Rep. Sp. Nov. **10**:431–444. 1912) has published several new species of flowering plants from China and the Sandwich Islands and includes a new genus (*Esquirolia*) of the Oleaceae from China.—I. M. LEWIS (Mycologia **4**:66–71. *pls. 58–61.* 1912) describes and illustrates a new black knot disease (*Bagniesiella Diantherae*) found on *Dianthera americana* at Austin, Tex.—J. LUNELL (Am. Mid. Nat. **2**:169–177, 185–188, 194, 195. 1912) describes new species and varieties in *Laciniaria*, *Toxicodendron*, and *Gutierrezia*.—T. H. MACBRIDE (Mycologia **4**:84–86. *pl. 62.* 1912) describes and illustrates a new *Geaster* (*G. juniperinus*) from Iowa.—T. MAKINO (Bot. Mag. Tokyo **25**:251–258. *pl. 7.* 1911) under the title of "Observations on the Flora of Japan" describes and illustrates a new genus (*Mitrastemon*) which represents a monotypic family (Mitrastemonaceae) of parasitic plants from the temperate regions of Japan, and regarded by the author as constituting an independent series (Mitrastemonales) most closely allied to the Aristolochiales.—U. MARTELLI (Webbia **3**:5–35. 1910) presents a synoptical revision of the genus *Freycinetia* of the Philippine Islands, recognizing 35 species of which 9 are indicated as new.—W. R. MAXON (Bull. Torr. Bot. Club **39**:23–28. 1912) records the results of a study of the genus *Phanerophlebia* and gives a key to the 7 recognized North American species.—W. MOESER (Rep. Sp. Nov. **10**:310, 311. 1912) characterizes a new genus (*Pseudobotrys*) of the Icacinaceae from New Guinea.—W. A. MURRILL (Mycologia **4**:72–83. 1912) in a fifth article on the "Agaricaceae of tropical North America" treats 13 genera and describes new species in *Mycena*, *Pluteolus*, *Conocybe*, *Naucoria*, *Cortinarius*, *Inocybe*, and *Hebeloma*. The same author (*ibid.* 91–100) gives a list of the Polyporaceae and Boletaceae collected on a recent tour of the Pacific Coast region; the article includes 8 new species of the former family and 4 of the latter.—J. A. NIEUWLAND (Am. Mid. Nat. **2**:178–185. 1912) describes two new species and four varieties of flowering plants, and (*ibid.* 201–247) in an article entitled "Our amphibious Persicarias" discusses several of the aquatic or semiaquatic smartweeds and proposes 2 additional species in the group.—J. M. GREENMAN.

Geotropism.—RITTER[3] applies the rotation method of PICCARD[4] for determining the distribution of geotropic sensitiveness in various grass seedlings. RITTER states that it is through the application of this brilliant conception alone that the distribution of geotropic sensitiveness has been settled in some cases.[5] In *Avena sativa*, *Hordeum vulgare*, and *Phalaris canariensis*, a short tip zone of the coleoptile is very much more sensitive than the basal region, which shows some geotropic sensitiveness. In *Avena* the very sensitive zone is 3 mm. long, and in *Hordeum* and *Phalaris* 4–5 mm. In *Setaria italica* all regions of the coleoptile are equally sensitive, while in *Sorghum vulgare* the tip region shows slightly greater sensitiveness. Since the main curving is in the epicotyl, a conduction of the stimulus to that region from the coleoptile must occur. The distribution of the motile starch in all these organs corresponds closely with the distribution of geotropic sensitiveness, so that RITTER considers the work confirmatory of, or at least not antagonistic to, the statolith starch theory.

In a study of the geotropism of rhizoids carried out in HABERLANDT'S laboratory, BISCHOFF[6] comes to the following conclusions: The rhizoids of the growing gemmae of *Marchantia polymorpha* and *Lunularia cruciata* are, contrary to the conclusion of WEINERT, positively geotropic, and those of the thalli show the same character with lower sensitiveness. BISCHOFF asserts that the lack of motile starch in these rhizoids does not necessarily argue against the statolith theory, for other motile bodies may take its place. The rhizoids of ferns are ageotropic. The main rhizoid of mosses (*Bryum capillare*, *B. argenteum*, and *Leptobryum pyriforme*) is positively geotropic in light, while the protonemata and side rhizoids are ageotropic. In the mosses statolith starch is found in the main rhizoid.

JOST and STOPPEL[7] have established the interesting fact that under high centrifugal force of sufficient duration the roots of *Lupinus* give the negative geotropic response instead of the positive. For negative response 16 gravities or more are needed for decapitated roots, and 70 gravities or more for intact ones. This lines geotropic response up with OLTMANN'S findings for heliotropic response; one and the same organ responds either positively or negatively, depending upon the strength of the stimulus. Parallel with heliotropism a

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[3] RITTER, HERMAN VON GUTTENBERG, Über die Verteilung der geotropischen Empfindlichkeit in der Koleoptile von Gramineen. Jahrb. Wiss. Bot. **50:** 289–327. *fig. 1.* 1912.

[4] PFEFFER, W., Physiology. English ed. **3:** 418–419. 1905.

[5] See review of DARWIN in BOT. GAZ. **46:** 387. 1908; also review of HABERLANDT in BOT. GAZ. **47:** 482–483. 1909.

[6] BISCHOFF, HANS, Untersuchungen über den Geotropismus der Rhizoiden. Beih. Bot. Centralbl. **28:** 94–133. 1912.

[7] JOST, L., and STOPPEL, R., Studien über Geotropismus. II. Die Veränderung der geotropischen Reaktion durch Schlenderkraft. Zeitsch. Bot. **4:** 207–229. 1912.

medium intensity of the stimulus produces no reaction; also the positive curving occurs in the zone of most rapid growth, while the negative takes place in the region of greater maturity. The *quantity of stimulus law* already established for heliotropism and geotropism[8] is confirmed by this work. The quantity of stimulus necessary for a negative response is about 1000 times that necessary for a positive response.

JOST[9] takes up the several positive arguments that have been offered in favor of the starch statolith theory, and with some partisanship shows their shortcomings. He observes that the negative argument is often used; that while many facts do not aid in substantiating the theory they at least do not disprove it. This statement holds, he asserts, because the theory itself has experienced a gradual process of adaption to the demands of newly established facts, which makes the theory of 1909 quite a different thing from that of 1900. In its earlier form the starch must actually fall on the *Plasmahaut* and lie there for some time to induce the reaction, while in the later form movement of the starch without geo-perception is explained by lack of irritability of the plasma, and geo-perception without movement of starch is explained by saying that actual displacement of the starch is not necessary for perception.

The author has studied the response of the root on the Piccard centrifuge and the effect of the removal or injury of various regions of the root tip on geo-perception and geo-response. The results on the Piccard centrifuge agree with those of HABERLANDT,[10] though the author gives them a different interpretation, which he believes accords better with all the facts known. Any injury that leaves the root tip attached or removes 0.5–0.75 mm. gives a wound effect that hinders geo-response for some hours. Removal of 1 mm. or more of the tip hinders geo-response for many days. JOST believes removal of 1 mm. or more of the tip affects the response in three ways: by wound shock, by removing a highly sensitive geo-perceptive region, by removing a region of great tonic significance in rendering other regions sensitive. His main evidence for the tonic effect of the tip 1 mm. is the fact that on the Piccard centrifuge the tip must extend over the point at least 1.5 mm. to give a reaction in favor of the tip, showing considerable sensitiveness in the growth zone; while removal of only 1 mm. of the tip renders the growth zone ineffective. The author believes that NĚMEC's conclusion that statolith starch is necessary in the tip for geo-perception lacks evidence, and that such a conclusion was drawn because NĚMEC failed to recognize the important tonic effect of the tip 1 mm. JOST believes that the meristem of the tip, along with the cap region immediately bordering on it on the one hand and the growth region on the other, are the regions of the maximum sensibility, while other regions may perceive but give

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[8] See review of BLAAUW in BOT. GAZ. **49**: 238. 1910.

[9] JOST, L., Studien über Geotropismus. I. Die Verteilung der geotropischen Sensibilität in der Wurzelspitze. Zeitsch. Bot. **4**: 161–205. 1912.

[10] See review in BOT. GAZ. **47**: 482. 1912.

no results unless the tip is present. The meristem in *Lupinus*, the form used, is starch free, consequently this interpretation which seems to agree well with all facts observed is opposed to the starch statolith theory.—WILLIAM CROCKER.

Gummosis.—SORAUER,[11] in two extensive papers, discusses gum-flow in the cherry and related phenomena in some other trees. He concludes that the tendency to gummy degeneration is latent in the cherry tree, and that stimuli such as frost and wounds only accentuate a natural tendency. Individual cells in the pith and bast, which in perfectly normal twigs of various trees show swelling of the walls and discoloration and degeneration of the contents, exhibit the primary evidences of the tendency to gummosis. Through variations in growth that may be regarded as normal, such as unusual breadth of the medullary rays, or through variations in nutrition affecting turgor, or through wounds, effects of frost, etc., the tension relations between pith and wood, and between wood and bark, are frequently greatly altered, resulting in release of pressure at certain points. At these points, islands of parenchymatic cells are regularly formed, among and in place of the normal prosenchymatic cells. This is a common phenomenon in many trees, without gummosis following; but in the cherry such islands of cells are the usual foci of gummy degeneration. They are particularly numerous in the wood formed by late fall growth; consequently different parts of the same branch or tree vary enormously in the tendency to gummosis.

Cells having the tendency to gummosis are deficient in starch, thin-walled, with heavy deposits of tannin and phloroglucin; in a word, they are cells which fail to mature. The cause of degeneration may be regarded as an excess of enzymes; degeneration in the individual cell starts in the cell contents, and extends to the secondary membrane, which swells and furnishes the chief material for the gum. As the gummosis extends to adjacent cells the order is of course reversed, the intercellular substance being first attacked, the cell contents last.

The bulk of these papers is devoted to a minute description of the histology and microchemical reactions of a great quantity of material illustrating various aspects of the gummosis problem. In addition to various species and varieties of *Prunus*, the following species are studied: *Corylus avellana*, *Pinus Laricio*, *P. silvestris*, *Fagus silvatica*, *Fraxinus excelsior*, *F. Ornus*, *Syringa vulgaris*, *Cytisus Laburnum*, *Tilia* sp., *Ampelopsis* sp., *Platanus* sp., and the pear. Scant attention is given to the work of previous investigators. These papers are of great value for the abundance of detailed observations, but the logic of the deductions is at times difficult to follow.

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[11] SORAUER, PAUL, Untersuchungen über Gummifluss und Frostwirkungen bei Kirschbäumen. Landwirtsch. Jahrb. **39**: 259–297. *pls.* 5. 1910; and **41**: 131–162. *pls.* 2. 1911.

BUTLER[12] rejects the earlier view of BEIJERINCK and RANT, that gummosis is due to a cytase which, unable to attack the wall of a living cell does so as soon as the cell is injured from any cause. He also rejects RUHLAND'S view that the gum is an oxidation product of carbohydrates and that gummosis is caused by admission of air through wounds. BUTLER considers that "gummosis is due to hydrolysis of the walls of the embryonic wood cells, which develop into a susceptible tissue." The form of development of a spot of gummosis shows, however, that it is correlated with release of pressure of the cortical tissues. Gummosis does not occur unless the cambium is growing actively and there is an abundant supply of water available to the roots; when these two conditions are present gummosis may develop "autogenously" or be induced by any sort of injury that stimulates growth of the cambium. Contrary to previous investigators, BUTLER states that starch and other cell contents play no part in gum formation. "Gummosis of *Prunus* and gummosis of *Citrus* are indistinguishable maladies." Both squamosis and exanthema are considered to be forms of gummosis. An excellent bibliography is appended.—HAVEN METCALF.

Root habits of desert plants.—In studying the roots of plants growing near the Desert Laboratory, Tucson, Ariz., CANNON[13] has made a rather detailed investigation of more than 60 species, including winter and summer annuals as well as various types of perennials. Three general types of root systems are recognized, namely, a generalized system with both tap and lateral roots well developed, a specialized type with the tap root the chief feature, and a second specialized type in which the laterals, placed near the surface of the ground, are especially well developed. The cacti are almost the sole representatives of the last type, and represent a specialization of a xerophytic form capable of absorbing a water supply from rains which penetrate a few centimeters only. This type seems necessarily limited to plants with very considerable water-storage capacity. A further specialization in the roots of most cacti is to be seen in the development of an anchoring and an absorbing system.

Plants having prominent tap roots include comparatively few species. They are mostly perennial in habit and limited in their distribution to areas with considerable depth of soil. In contrast, the generalized system is characteristic of the majority of both the perennial and annual species. It facilitates distribution because of its plasticity, and because its representatives are found in widely varying situations. It is to be regarded as the least xerophilous of

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[12] BUTLER, ORMOND, A study on gummosis of *Prunus* and *Citrus*, with observations on squamosis and exanthema of the *Citrus*. Ann. Botany **25**: 107–153. *pls. 4.* 1911.

[13] CANNON, W A., The root habits of desert plants. Carnegie Institution of Washington. Publ. No. 131. pp. 96. *pls. 23.* 1911.

the three systems, and hence includes almost all the annual plants. Few of these annuals penetrate the soil deeper than 20 cm., and most of the lateral branches are less than half this distance from the surface. Competition is evident between the various members of the generalized type, and also between them and those of the first specialized class. The best development of root systems is found in the summer annuals, due to more favorable vegetative conditions, and particularly to more favorable soil temperature during that portion of the year.

The details of root development in the various species are illustrated by many photographs and drawings, while the detailed descriptions contain many interesting facts concerning the different plants.—GEO. D. FULLER.

Chromatophores and chondriosomes.—FORENBACHER[14] has made a study of the origin of chloroplasts and leucoplasts in the stem and root of *Tradescantia virginica*, the object of which is to show the origin of these structures from chondriosomes (filamentous mitochondria). Beginning with the fully formed chloroplasts of the stem cortex and leaves and proceeding toward the tip, he finds a complete gradation between the fully formed chloroplasts and the chondriosomes. The intermediate forms present themselves as dumbbell and granular structures which gradually pass over into the chromatophores. Similar gradations are found between the chondriosomes (mitochondria) of the root tip and the leucoplasts. This work thus confirms the results of PENSA and LEWITSKY and those of GUILLIERMOND on the origin of the chloroplasts from mitochondria (chondriosomes).

Some doubt is justified of the efficiency of the methods employed for demonstrating the chondriosomes of plant cells. MEVES, for example, found these structures in the tapetal cells of *Nymphaea*, but not in the spore mother cells, in which, however, by suitable methods they may be shown to be very numerous. The reason was the small power of penetration of the fixing fluid, which did not reach the deeper tissues before the mitochondria had undergone change or disappeared. In eliminating acetic acid wholly from his fixing fluid, FORENBACHER has diminished its already slight power of penetration. His figures are not convincing, for the structures labeled as chondriosomes do not conform in shape or number to the usual condition in rapidly dividing cells of higher plants. It is quite possible that his young chloroplastids do not belong to the category of mitochondria (chondriosomes) at all.—R. R. BENSLEY.

Vascular anatomy of Salicales.—Miss HOLDEN[15] has investigated the position of Salicales on the basis of the vascular anatomy of the North American

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[14] FORENBACHER, AUREL, Die Chondriosomen als Chromatophorenbildner. Ber. Deutsch. Bot. Gesells. **29:**648–660. *pl. 25.* 1911.

[15] HOLDEN, RUTH, Reduction and reversion in the North American Salicales. Ann. Botany **26:**165–173. *pls. 20, 21.* 1912.

representatives. In the ENGLER arrangement, based on floral characters, they are one of the three most primitive groups of the Archichlamydeae. Most of the eastern representatives of the group have uniseriate rays and "terminal" parenchyma ("only at the end of the annual ring") in the stem cylinder, but in the conservative regions multiseriate rays and vasicentric parenchyma are found. This latter combination is found also in the stem cylinders of certain western forms. The conclusion from these facts is that multiseriate rays and vasicentric parenchyma represent the primitive condition of the group, and that their present simple structure is due to a reduction from a more complex structure. This means that, according to the testimony of vascular anatomy, the Salicales should be transferred from a very low position to a relatively high one among the Archichlamydeae.—J. M. C.

The fruit of Compositae.—LAVIALLE[16] has begun the publication of a volume of observations on the development of the wall of the akene of the Compositae, a complex of testa and pericarp. The first chapter and part of the second have appeared in the *Annales* as cited. Since 298 species, representing 65 genera, have been studied, the number of observations are very great. Just what the value of them will be is also obvious. In the account of the "actual state of knowledge of the structure of the fruit of Compositae," the actual state of knowledge of the author is very apparent. The citations are few, and apparently no contributions in English were available.—J. M. C.

A new Cordaites.—Miss BENSON[17] has described a new species of *Cordaites* from a fairly well preserved specimen obtained from the coal mines at Shore, England. It is compared with related species, and the intimation is given that along with *C. Wedekindi* Felix it may represent a new genus, whose seeds are already suspected to be those of a *Mitrospermum* closely associated with it in the deposit. The whole leaf is said to have "a markedly xerophilous character."—J. M. C.

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[16] LAVIALLE, P., Recherches sur le développement de l'ovaire en fruit chez les Composées. Ann. Sci. Nat. Bot. IX. **15:** 39–64. 1912.

[17] BENSON, MARGARET, *Cordaites Felicis*, sp. nov., a cordaitean leaf from the Lower Coal Measures of England. Ann. Botany **26:** 201–207. *pl. 22. fig. 1.* 1912.

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Editor: JOHN M. COULTER

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THE LIFE HISTORY OF ANEURA PINGUIS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 159

GRACE L. CLAPP

(WITH PLATES IX–XII)

Historical

In his classical study of liverworts, LEITGEB (19) has given a comparative treatment of the genus *Aneura*. Stages of development chosen from several species picture the life history of the genus rather than that of any one species from spore to spore. HOFMEISTER (13) earlier described the apical cell and sex organs of *Aneura pinguis*, and KNY (15) worked out in an elaborate scheme the segmentation of its apical cell. LE CLERC DU SABLON (18), GOEBEL (10–12), CAMPBELL (3), and CAVERS (4) have since added facts, but gaps have been left in the continuous development, chiefly in the embryogeny and in the growth of the sporeling.

Material

Material of *Aneura pinguis* was collected by Dr. LAND at Xalapa, Mexico, in the autumns of 1906, 1908, and 1910. The region around Chicago has offered abundant supply for field study. The plants were killed in the field in Flemming's fluid (weaker), in alcohol (50 per cent) and formalin, and in chrom-acetic acid without osmic acid. Following the close series of alcohols in dehydration, the material imbedded in paraffin was cut in sections 3–10 μ thick. Safranin and anilin blue, Haidenhain's iron-hematoxylin with and without Magdala red, and Flemming's triple stain were used for

stains. Shrinkage in the young embryo and resistance to infiltration of the mature capsule were the chief difficulties met.

Thallus

SCHIFFNER (**23**) describes *Aneura pinguis* as a cosmopolitan species, strictly dioecious. LAND reports the growth of the species on decayed fallen logs in the rain forest as most luxuriant. The plants exceed only slightly, however, those growing in the hydromesophytic habitats of Chicago. On fallen hemlock logs in shady ravines and on the mossy edges of pine-oak dunes bordering sloughs the plants form a close mat. Wherever moss forms a humus layer along the lines of seepage of the clay bluffs along Lake Michigan, the thalli are also found. In the prairie meadows *Aneura pinguis* often extends half an inch on *Typha* and *Acorus* leaves or grows on clumps of exposed grass roots. In all these places moisture, diffused light, and fairly low temperature are the favorable conditions for its growth. Plants grow fairly well in the laboratory when these conditions are imitated.

Aneura pinguis is strictly dioecious, but both kinds of plants grow side by side in the field, often with margins overlapping (fig. 1). In general the thallus is a flat ribbon-shaped plant closely appressed to the ground, with frequent branches, and slight indentations along the margins. While it averages 5–7 mm. in width, it may be reduced when growing in a moist chamber with light from one side in the laboratory to less than 2 mm. (NĚMEC **21**).

The thallus consists of compact cells, unequally elongated in the direction of the main axis of the plant. Although it lacks a midrib, the plant is usually thicker along the center, thinning out toward the lateral margins. All the cells contain chloroplasts at some time and the plastids often have 5 or 6 starch grains. Ordinarily it is 10–12 cells thick. There is no definite differentiation into tissues, but the superficial layer is clearly composed of smaller cells with a larger number of chloroplasts. This dorsal "small-celled epidermis" has undergone one more division, longitudinally and transversely vertical, than the layers beneath (fig. 2). Plants in the shade appear succulent and are deep emerald green in color. The numerous chloroplasts are found dividing as often as in *Funaria* or *Elodea*.

On the ventral surface rhizoids (figs. 13–15) and mucilage hairs (fig. 12) indicate slight cell differentiation. The rhizoids contain chloroplasts at first like the other superficial cells (fig. 13). Such cells project slightly, elongate, the chloroplasts disappear, and the rhizoids look like root-hairs. As they grow longer the position of the nucleus changes and the cytoplasm varies in amount and distribution. Both are near the somewhat thickened tip when the rhizoid is old. The rhizoids resemble root-hairs in that they become irregularly lobed in contact with soil particles (fig. 15) and flatten out in a most deformed way against other thalli and bark. BOLLETER (**2**) notes this same lobing in *Fegatella conica* and it is common among liverworts. The length and number of rhizoids varies greatly. In contact with an underlying thallus or bark they are very short (0.09–0.16 mm.); in soil and moist air they average less than 1 mm., and only occasionally reach 2 mm. On closely appressed plants the rhizoids are numerous and scattered; in soil they grow along the central axis but are never definitely localized. Irregularity may come from fungi in the rhizoids, and again they may be as straight as if uninfected. In no case were the lobes of the rhizoids cut off by walls.

Gemmae have been described by many for *Aneura pinguis*. In the material at hand no gemmae were found. If they are characteristic of this species, their absence must be due to the conditions under which the plants grew. EVANS (**7**) has found in species of *Metzgeria* that gemmae are not likely to appear when the plant is growing luxuriantly. This would account for their absence in the field, but one might expect them to appear on plants grown under less favorable conditions in the laboratory.

Increase in the number of plants is brought about, as in many other thallose liverworts, by the dying away of older parts, when branches become the main axes of new individuals.

Aneura pinguis produces three kinds of branches, the ordinary vegetative ones and those bearing the two different sex organs. Such branches have their origin in the segments of the apical cell. All of the descriptions of this cell agree that it cuts off segments on two sides alternately right and left (figs. 3–11). Vertical sections through any of the marginal indentations which indicate

growing points show clearly that its longer axis is the vertical one (fig. 2).

Very rarely at the forward end of the thallus can only one apical cell be found (figs. 5, 6). Usually two indentations are separated by a narrow marginal projection and each sinus contains two apical cells (figs. 9–11). One set carries on the main axial growth, the other produces a branch. The apical cell of the branch originates in a segment of the axial apical cell by a curved vertical wall bent to the right or left so that it strikes the wall of the segment opposite the last cutting one.

The more rapidly growing dorsal surface carries the apical cell to the ventral side (fig. 2). The wall-formation in either direction, therefore, shows an obliquity which later is distinctly vertical or horizontal. The primary segment is divided by a vertical transverse wall into an inner posterior cell and an outer anterior marginal one. Walls parallel to the surface come in now, followed by more vertical ones. The order of vertical, transverse, or longitudinal does not seem fixed. Clearly these three directions give thickness, length, and width to the thallus.

If the growth of two apical regions is nearly equal, the thallus appears dichotomously branched; if one grows faster, the other is recognizable as an indentation on the lateral margin, where it may remain growing very slightly if at all; or if the main axis be injured, it becomes the apical region of the main thallus, growing rapidly.

Characteristic of the apical cell are the mucilage hairs borne on the ventral surface of the thallus (fig. 12); 6–10 of them curve inward and upward around the growing point. KNY and LEITGEB describe the mucilage cells as bearing no direct relation to the thallus in arrangement. They show an alternation, however, corresponding to that of the apical cell segmentation. The superficial cell from which the hair originates first projects from the surface, and then divides into two cells. The basal inner cell retains its plastids permanently; the chloroplasts of the outer one, after some growth, are transformed into a mucilaginous stuff, which stains very deeply. These are the hairs which are sloughed off as the thallus grows. The basal cell divides like any superficial cell. Apparently it is the posterior ventral surface cell, cut from the

primary segment by a vertical transverse and horizontal wall, which produces it.

Sex organs

ANTHERIDIA.—The antheridia of *Aneura pinguis* are borne in the upper surface of lateral branches which occur singly, in groups of three, or occasionally in groups of two. On the branch their arrangement is extremely regular, in two alternating rows corresponding to the segments of the apical cell. They appear imbedded because of the rapid marginal growth of the surrounding cells.

LEITGEB'S diagram for their arrangement in *Aneura palmata* holds true also for *Aneura pinguis*. After the division of the primary segment into an outer marginal and an inner posterior cell by a vertical transverse wall, and after horizontal cleavage of the latter into a dorsal and a ventral cell, the dorsal cell by a vertical longitudinal division forms an inner (toward the median axis of the thallus) and an outer (toward the lateral margin) cell. The inner by a transverse vertical cut divides into two cells, the anterior of which gives rise to the antheridium. This dorsal superficial cell (the antheridium initial), containing a large nucleus and abundant cytoplasm, enlarges and projects (fig. 16). It divides into two cells, the outer of which, by a horizontal wall, forms a stalk cell usually dividing once at least, and the antheridium mother cell (fig. 17).

The method of development follows the *Jungermannia* type. First a vertical wall divides the outer cell into two equal halves (fig. 18). By two vertical intersecting walls in each half, a wall layer of four cells surrounds two central cells—primary spermatogenous cells (figs. 22, 23). By rapid growth the antheridium becomes spherical and appears transparent (fig. 26). Its wall cells, however, contain chloroplasts which persist until the sperm mother cells are distinguishable. The wall cells of the upper half grow noticeably larger than those of the lower half.

No definite cytological study of spermatogenesis was made, but some few points were noted. No centrosome was evident during any division of the spermatogenous cells. The diagonal division of the sperm mother cells separates them by a membrane which

stains as deeply as does the cell wall of the mother cell. The oval nucleus stains deeply and soon occupies one end of the protoplast (fig. 27). At the other end, a dark spot appears in the cytoplasm—the blepharoplast—which gives rise to the cilia. The nucleus in its growth elongates, soon making a turn around the cytoplasm. The cilia are not easily distinguished from the coils of the nucleus. Beside the beak of cytoplasm, anterior to the nucleus from which the cilia extend, a rounded mass is left at the posterior end of the sperm. This is a mechanical hindrance to the movement of the sperms when the cell walls are transformed into a mucilaginous substance and the sperm is often twisted into small spirals on its own axis (fig. 27). These disappear as soon as space is given, and at the time of shedding the mass of cytoplasm at the base is also gone. The body of the sperm is very long and averages about 2.5 times that of the cilia. Cilia 35.2 μ and sperm 88.7 μ, in rough figures, were the measurements of the longest sperms squeezed out of the antheridium before it had burst naturally. Probably when shed in the field they have grown somewhat longer.

The antheridia begin to form early in the spring. They develop in acropetal succession until August, when many of the branches, as has been noted (LEITGEB, CAMPBELL), continue vegetative growth. The last antheridium formed is sometimes not imbedded, but superficial, owing to the rapid elongation of the thallus.

ARCHEGONIA.—*Aneura pinguis* bears its archegonia also on the dorsal surface of distinct lateral branches (fig. 28). Such plants have conspicuously light green filamentous outgrowths, varying in length and width on the lateral margins. These are caused by the more rapid growth of the thallus edges of the main axis or of the lateral branch. Again, there may be from one to three branch primordia; usually, however, one outstrips the others in development. Like the antheridia, the archegonia are regularly arranged in two rows, alternating according to the apical cell segmentation. The division of the primary segment is as usual. The first dorsal superficial cell is the archegonium initial. In order of development it follows the general liverwort type. Three vertical intersecting walls surround a central cell from which a cap cell is cut off by a horizontal wall (fig. 29). The central cell gives rise to four neck

canal cells, a ventral canal cell, and the egg cell. The archegonium wall has two layers of cells (figs. 32, 33). The 4–6 canal cells are of short endurance; their walls break down and the cytoplasm and nucleus are transformed into a mucilaginous substance. The egg cell is large and round, its cytoplasm containing many starch grains (fig. 33). When the cap cells bend back, there is a clear passage made in the neck to the egg. Fertilization was not observed.

As soon as fertilization has occurred, the neck and venter cells divide rapidly, and the whole branch is a thick cushion of cells projecting beyond the margin of the thallus. Usually only one embryo grows on a branch, and where two appear they probably belong to two branches. Two have been reported, however, in one calyptra (COKER **6**). Occasionally archegonia, immature and after the egg has been fertilized, are carried with the filaments to the top of the calyptra in its growth. LEITGEB thinks more trichomes are produced on the torus, but this seems unlikely, for many are sloughed off as it develops. Some new rhizoids do grow at the bulbous base.

Sporophyte

The first division of the egg is a transverse one into epibasal and hypobasal cells (fig. 34). The hypobasal cell has been said either to form a few divisions or to grow into a lobed haustorial cell (LEITGEB **19**). It distinctly becomes a true haustorium (figs. 35, 36), rhizoidal in form. Both cells elongate rapidly; the haustorium sometimes lobes and sometimes remains straight. The epibasal cell is divided by a horizontal wall into two cells (fig. 35) containing abundant cytoplasm, many plastids, and large nuclei. In this three-celled stage disorganization of the cells of the calyptra around the base of the suspensor is striking. The uppermost cell divides again by a horizontal wall, so that a filament of four cells is formed, including the haustorium. Vertical walls now come in, so that there are three rows of quadrants (fig. 36).

The lowest tier next the haustorium now forms two rows (figs. 37, 38), its vertical and transverse walls having no definite sequence. It corresponds to the foot, and the cells form at first a more compact

mass than the slender ones above. The uppermost cell arising in the epibasal row divides to form the capsule; the middle originates the seta, probably by its intercalary growth as LEITGEB has suggested. When, therefore, the seta consists of three or four tiers of cells, the capsule is definitely differentiated. It consists of two rows, each of eight cells. Periclinal walls have cut out a wall layer one cell thick (fig. 38), leaving a central sporogenous tissue of eight cells. The lower four divide by horizontal and vertical walls; the upper also divide, but form only a group of sterile cells—a cap, later continuous with the elaterophore. The wall of the lower half becomes two layers by periclinal divisions not at all simultaneous (figs. 39, 40). The difference in rate of growth from now on is a striking feature of development in the capsule (LE CLERC DU SABLON **18**). It first shows in the contrast between the lower and peripheral region and the upper central part. The contents of the cells differ in size of nuclei and amount of cytoplasm. Cell divisions are in every direction. The capsule changes from spherical to oval and elongates rapidly (fig. 41). This difference in rate of growth accompanies the formation of the elaterophore, but what determines the rate? The more slowly dividing cells of the upper central region begin to elongate, and the elaterophore is outlined (fig. 42); its cells have smaller nuclei and less cytoplasm. Although cell divisions are fewer along its margin, they must still be considered sporogenous tissue. Diagonal divisions and radial arrangement of diamond-shaped cells indicate elongation of the capsule. Cells continuing the axis of the capsule between the elaterophore and the base are still rectangular, like those of the elaterophore except in size of nuclei.

Differentiation among the spindle-shaped cells is the next evidence of separation of the sporogenous tissue into elaters and spore mother cells (figs. 43–50). While in the central axis the elongated diamond-shaped cells appear to form continuous rows to the base, in the radial peripheral regions this is more uncertain. The next stage, and a most unsatisfactory one for study, shows a partial transformation of the walls of the elaters and of the spore mother cells. The elaterophore forms a central cylinder of long prosenchymatous cells, the marginal ones of which have a free tip.

They contain plastids with starch. The protoplasts of the elaters and spore mother cells are outlined by a definite membrane at a distance from the wall. The space between, however, shows less well defined strands. The nucleus of the elater is large (figs. 44, 45), at the center, extending well across the diameter of the cell. There are plastids in the elaters, and BOLLETER (**2**) considers the elaters in *Fegatella* feeders of the spore mother cells because the starch disappears from the elaterophore about this time. The spore mother cells also have very large nuclei and the form of the cell is irregularly rectangular to triangular.

The difference in rate of growth noted before between the peripheral and central regions is much more evident at this stage. The four lobes of the spore mother cells are well rounded toward the outer portions of the capsule, while those at the center are just beginning to be distinct. The nucleus with a clear nucleolus lies at the center of the lobed cell (fig. 46). Two successive divisions of the nucleus form the tetrad of spores.

The cell plate becomes continuous with the deeply staining membrane of the lobes. This membrane soon differentiates into another substance, being added to from the interior where its outline is very irregular. Centrally between the two margins staining indicates lines of some substance which grow out to the outer margin, forming at first irregular projections. Meanwhile, within the protoplast a cellulose layer forms. When the spore is mature the two wall layers are not distinct (figs. 51, 52). The protoplast containing chloroplasts seems to be surrounded by a single brown wall with echinate projections. During this time the elaters have changed. The cytoplasm has come to form a spiral along the wall and a broad brown thickening takes its place (fig. 52). Two spirals are not rare and the elaters are often branched (JACK **14**). Probably examination of the chemical changes taking place in the spore coat would find them similar to those BEER (**1**) has found for *Riccia*.

The cell walls of the elaterophore are thickened in a narrow single spiral. The two wall layers have ring thickenings in the sterile cushion at the apex, and in the two upper layers of cells of the seta irregular thickenings are found. The lines of dehiscence are

remarkably distinct in cross-section (fig. 54), for the walls do not change on that side, but remain thin, composed of cellulose.

The seta, measuring about 2 mm. in length, would be described as having a club-shaped foot if it can be called a foot. Even when the seta consists of a few tiers of cells, the glandular appearance at the base is striking. Tissues of the calyptra and seta disorganize so that at the base of the seta there are always some glandular cells and others very much crushed. During its growth the bulbous base of the gametophyte and sporogonium has turned from a horizontal to a vertical position.

The capsules dehisce progressively along the thallus from early spring (March) through May. GOEBEL (**10**) has well described the dehiscence and shedding of spores in *Aneura palmata*. The seta elongates rapidly (NĚMEC **20**) from 2 to 30 and more mm., in the field often twisting on its own axis. Individually its rectangular cells lengthen from 60 μ to 500 and 600 μ. This pushes the capsule far beyond gametophyte and calyptra. Along the well marked lines between the valves, about one-third of the way from the tip at the greatest width of the capsule, a splitting begins. The crack lengthens until with a jerk the valves are bent back. Some spores are freed now, but the majority are shed by the next movement of the valve, when its fourth of the elaterophore springs upward 45° or more. Spores and elaters fall together, the tetrad often complete.

Germination of spores

Plants with capsules about to shed were brought from the field March 23, April 15, May 17, and May 20, and put on wet cotton under bell-jars or in large Petri dishes. Spores were sown as soon as the capsules burst. On sterilized cotton the spores (averaging 60–68 or 70 μ) are soon lost. A better medium and more easily examined under the microscope is made by putting a layer of heavy white filter paper over wet cotton in a Petri dish. Porous clay plates are also good. Drop cultures in 0.5 and 1 per cent cane sugar, 2.5 and 3 per cent glucose, 0.5 and 1 per cent lactic acid, 0.3 and 0.6 per cent Knop solution, vegetable lipase, distilled water, all died after reaching the two-celled stage. The excessive amount of moisture was one cause of this, for cultures made at the

same time on cotton with distilled water and 1 per cent cane sugar lived. On moist cotton in the sunlight the spores died in the one-celled or two-celled stage. Other cultures, therefore, were kept in a room with the window open, so that the temperature varied roughly with that outside, and the light was kept diffuse by the window shade. Sowings were made on sterilized clay, sand, sphagnum, humus, and sand, and kept under bell-jars. Cultures on rotten wood were spoiled by *Pencillium*. Although the pots containing the soils were scrubbed, dried, sterilized over night in a drying oven above 115° and again with the soils in an autoclave, many became infected with a species of *Chaetomium*. This could have come about when spores were taken out for examination. The accompanying table records some of the data.

Sowing	Final examination	Time	Medium	Condition of spores
March 23...	June 23	3 mos.	H_2O on cotton	2-celled to all stages (fungi)
April 15...	June 17	2 mos.+	clay	1–3-celled; majority 2-celled
April 15...	June 17	2 mos.+	H_2O on filter over cotton	majority 2-celled
April 6...	June 19	2 mos.+	H_2O on filter over cotton	2-celled
May 5...	June 19	1 mo. +	H_2O on filter over cotton	2-celled
May 5...	June 17	1 mo.	soil	2–7-celled (fungus)
May 21...	June 21	1 mo.	sand	2-celled
May 21...	June 21	1 mo.	1% cane sugar filter on cotton	2-celled
May 29...	June 21	1 mo. —	soils	1–4-celled (Chaetomium)
May 29...	June 21	1 mo.	H_2O filter on cotton	2-celled
May 29...	June 21	1 mo.	filter over soil	2–4-celled (fungus)

This rough table shows that the rate of development is variable and slow. The spores of March 23–June 23 were shed in a heap on the moist cotton in the moist chamber containing the plants from the field. Here were found two-celled stages and thalli with branches. Uninfected plants have reached at most 4 and 5 cells, while those with fungi have mature thalli. This difference is apparently due to some change caused by the fungus.

LEITGEB (19) describes the germination of *Aneura pinguis* and *A. palmata*, but figures only the early stages of *A. palmata*. He

says that the spores enlarge strikingly at first, and by one-sided growth a filament is formed which elongates by apical growth, forming a cylindrical body. This body branches and in the tip cell of the main axis and its branches the typical apical cell of the mature thallus arises.

In *Aneura pinguis* the spores at shedding contain chloroplasts as mentioned above (fig. 51). The spore does increase rapidly in size from 60 and 70 μ to 90 and 100 μ in a few days. The plastids are grouped somewhat at one side, where the cell begins to elongate into a slight projection. A wall divides the spore into two unequal cells (fig. 56) (this may happen within 1 or 2 weeks); the smaller one grows until it equals the sister cell. The exospore has not been split, but has elongated and surrounds the two cells (figs. 57, 58). The younger cell is now divided unequally by a vertical wall bent slightly toward the long axis of the cell (figs. 59, 60). It soon grows as large as the cell from which it was cut off, and the division could easily be mistaken for an equal one. This division may also be horizontal, resulting in a dorsal and a ventral cell. The apical cell may originate in either one of these two cells, probably the better lighted one (PEIRCE **22**, LAMPA **16** and **17**, GOEBEL **10–12**, BOLLETER **2**, SCHOSTAKOWITSCH **24**). This second or third wall can then be considered the one which marks out the apical cell.

Only one sporeling was found where the exospore had split and a filament of five cells had grown (fig. 71). The next division comes when the last cell cut off equals that from which it was cut, and the new wall again is a vertical one inclined toward the axis of elongation (fig. 61). This mode of development continues up to the four- and five-celled stage. The only difference between this apical cell and that of the mature thallus is the longer time interval between the segmentation and the division of the segments. In this four- and five-celled stage the echinate projections of the exospore are still present, at a greater distance apart and finally disappearing. The mass of cells looks slightly as has been pictured for *Lejeunia serpyllifolia* (CAMPBELL **3**).

This then reduces *Aneura pinguis* to the condition described by GOEBEL (**12**) for *Metzgeria furcata*, where the filamentous stage or *Vorkeim* consists of one or two cells. The branched filaments are

lacking, which must depend upon the conditions of light and moisture under which they are grown.

Another interesting fact connected with the development of the spore is that the fungus plays some part in it when present. Where the spores fell from the capsule and germinated on the cotton, and in another case where the capsule did not open wide but spores in the line of the valves germinated, a fungus was found infecting the plants. These sporelings were all past the two-celled stage (figs. 64–66). The better lighted thalli were forked, possessing mucilage hairs and rhizoids. In whatsoever way the fungus affects the plant, development at least is hastened. Fungi have been noted in many leafy and some thalloid liverworts (NĚMEC **20,** BOLLETER **2,** GARJEANNE **8,** CAVERS **5**), but only in one case does GARJEANNE note a fungus with the spore, and then only as near it.

The infection begins in any cell of the sporeling (figs. 64–66) and extends irregularly along the lower surface. Large knots of hyphae are found in the cells. At first the cells are not killed, fungus, plastids, and nucleus all being present. Gradually the plastids disappear but the nucleus remains longer. In cells adjoining and near to the infected ones, starch of the plastids has been transformed into dextrine.

A majority of the plants of the field are infected irrespective of habitat. One would like to know whether spores are also infected early or whether the laboratory conditions were such as to favor infection. It is hardly probable that any such relation exists between spores and fungus as BRUCHMANN has found for species of *Lycopodium*. It is more likely, as GARJEANNE thinks, a chance condition, and not at all an endophytic fungus of mycorrhiza plants. Thalli from the field usually have the fungus a short distance behind the actively growing region, and sometimes extending along two-thirds of the dorsal surface. Is it possible that this is one of the main causes for the dying back of the thallus?

Rhizoids are commonly filled with strands of the hyphae (fig. 68). Infection of the rhizoids commonly occurs from the thallus, and when chloroplasts are still present. The elaborate pseudo-parenchyma of fungi described by NĚMEC (**20**) at the base of the rhizoids is lacking, but there are knots of hyphae. Rarely, also,

are the rhizoids as deformed by the fungus as by the obstacles in their path of growth.

Inoculations of pure cultures have not been made because of the desire to get as many sporelings as possible to develop mature thalli. Some of the fungi obtained pure were a species of *Fusarium*, *Cephalothecum roseum*, a species of *Alternaria* and of *Gloeosporium*, and an unidentified one which grew with *Pencillium* in an impure culture. GARJEANNE has found that more than one species may be present at the same time in a rhizoid. It will be interesting to know how many of the above can infect the spores.

Summary

1. The gametophyte of *Aneura pinguis* is a simple, slightly differentiated thallus.

2. Archegonia and antheridia are borne on lateral branches of dioecious plants; they develop according to the *Jungermannia* type.

3. The sporophyte of *Aneura pinguis* is highly specialized. One-half of the embryo at its first division forms a haustorial cell; from the other half capsule, seta, and a temporary foot develop. Sterilization of the tissue of the capsule occurs at three periods: (1) the wall and apical cushion are cut out; (2) the elaterophore is defined; (3) sporogenous tissue is differentiated into elaters and spore mother cells.

4. The capsule splits by four early defined valves. The spores are echinate and contain chloroplasts at maturity.

5. The protonemal stage is reduced to one or two cells. The spore coat incloses the very young sporeling.

6. The mature thallus often contains a fungus. Infection takes place in some sporelings as early as the two-celled stage. Rhizoids may be infected from the thallus.

7. No gemmae are found on *Aneura pinguis*. New plants are produced by the dying back of the old thallus.

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EXPLANATION OF PLATES IX–XII

FIG. 1.—Sketch of dioecious thallus.

FIG. 2.—Vertical longitudinal section through apical cell; ×505.

FIGS. 3–8. Serial horizontal section through apical cell; ×830.

FIG. 9.—Horizontal section of thallus, showing two apical cells; ×505.

FIGS. 10, 11.—Horizontal section of thallus showing two apical cells in one sinus; ×830.

FIG. 12.—Young mucilage hairs; ×830.

FIG. 13.—Young rhizoid with chloroplasts present; ×830.

FIG. 14.—Young rhizoid infected by fungus from within; ×830.

FIG. 15.—Rhizoids with and without fungus, showing irregular form; ×175.

FIG. 16.—Vertical section through antheridium initial; ×505.

FIG. 17.—Vertical section, showing antheridium initial divided into stalk and antheridium proper; ×830.

FIG. 18.—Vertical section through antheridium, showing first vertical wall; ×505.

FIG. 19.—Stages of development in antheridium, showing wall and spermatogenous cells defined; ×505.

FIG. 20.—Vertical section through antheridium, showing early divisions of the spermatogenous cells; ×830.

Figs. 21–24.—Horizontal sections through the antheridium, showing its development; ×1650.

FIGS. 25, 26.—Vertical sections through older antheridia, showing stalk cells, and fig. 26 showing the development of the tissue around the antheridium; ×505.

FIG. 27.—Stages of development in the sperm; ×2800.

FIG. 28.—Horizontal section through an archegonial branch, showing numerous archegonia; ×505.

FIG. 29.—Vertical section through young archegonium; ×830.

FIG. 30.—Vertical section through older archegonium; ×830.

FIG. 31.—Horizontal section through archegonial neck; ×830.

FIG. 32.—Vertical section through mature archegonium; ×830.

FIG. 33.—Vertical section through archegonium, showing canal cells disorganized; ×830.

FIG. 34.—First division of the young sporophyte; ×1040.

FIG. 35.—The haustorial cell of the sporophyte, well elongated, and gametophyte cells disorganizing; ×1040.

FIG. 36.—Haustorial cell more elongated; the sporophyte proper composed of four cells; ×1040.

FIG. 37.—Foot, seta, and capsule region of the sporophyte marked out; ×1040.

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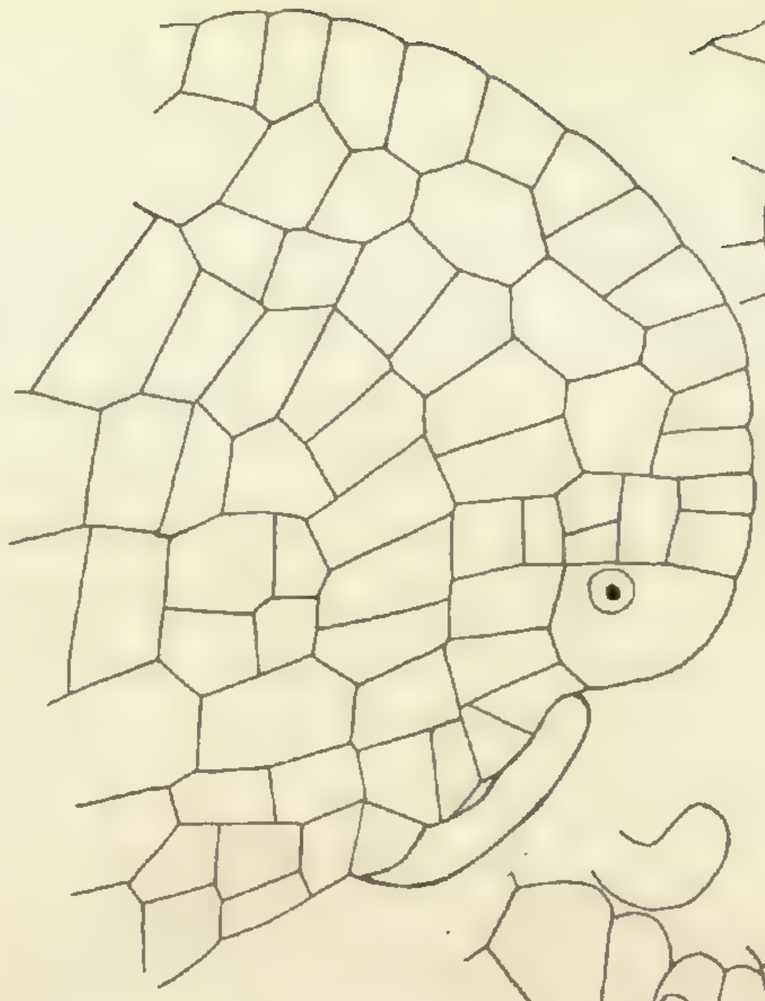

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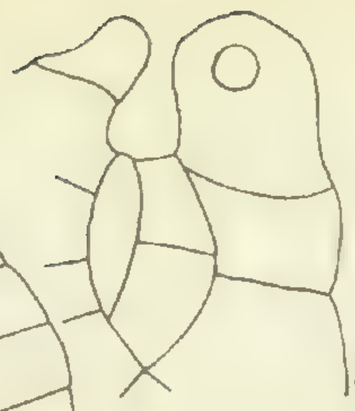

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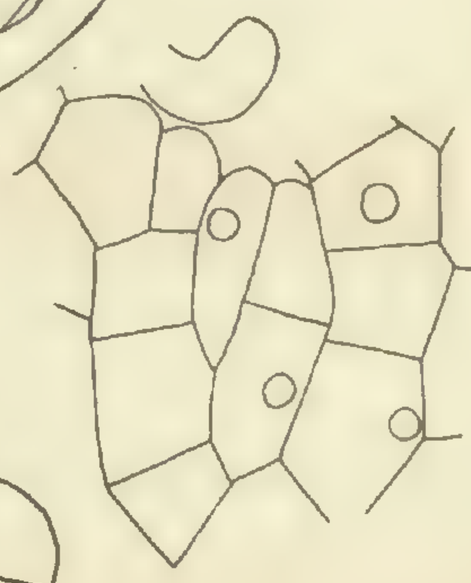

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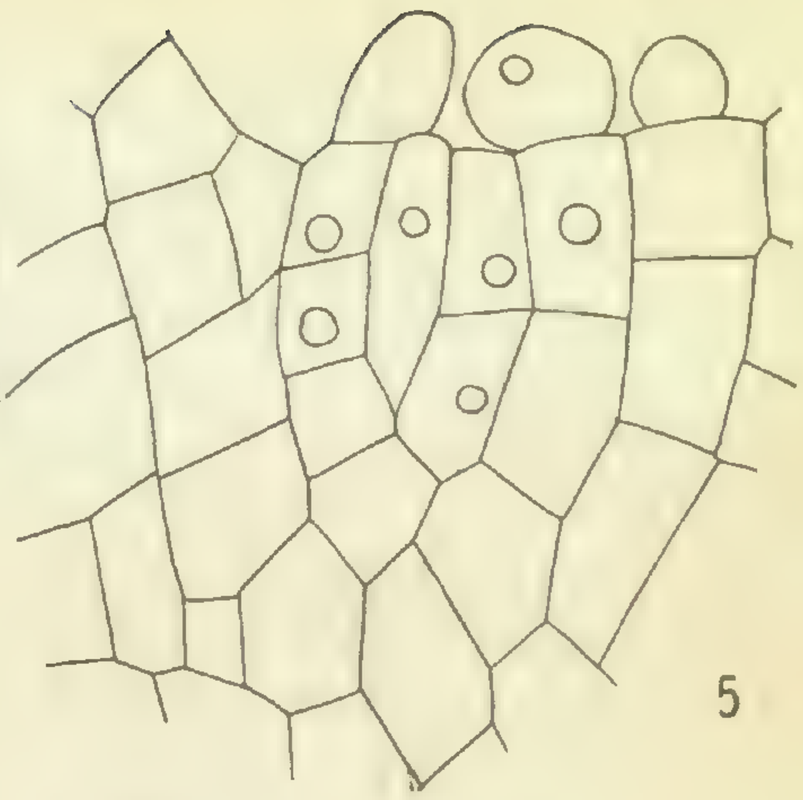

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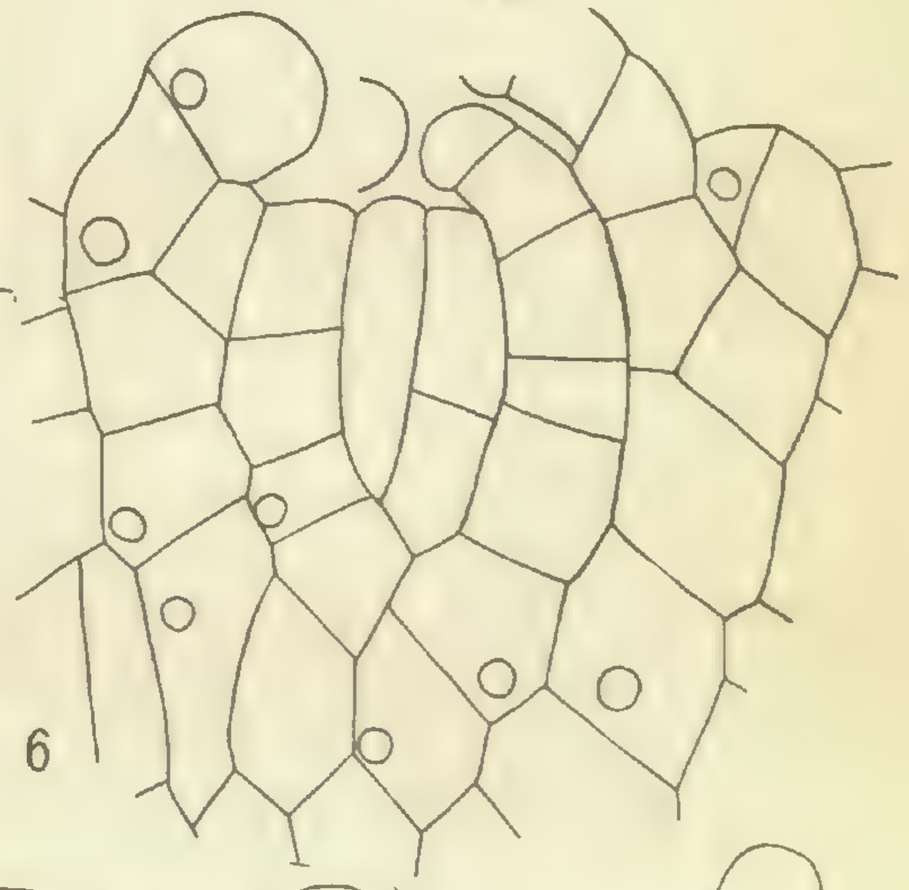

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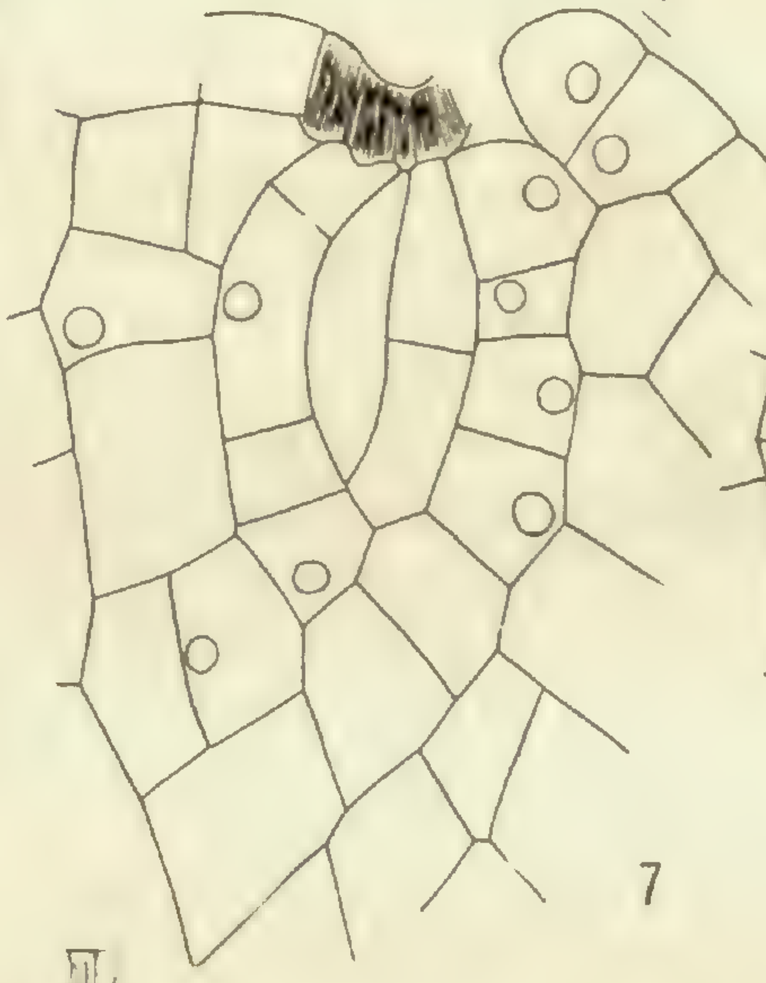

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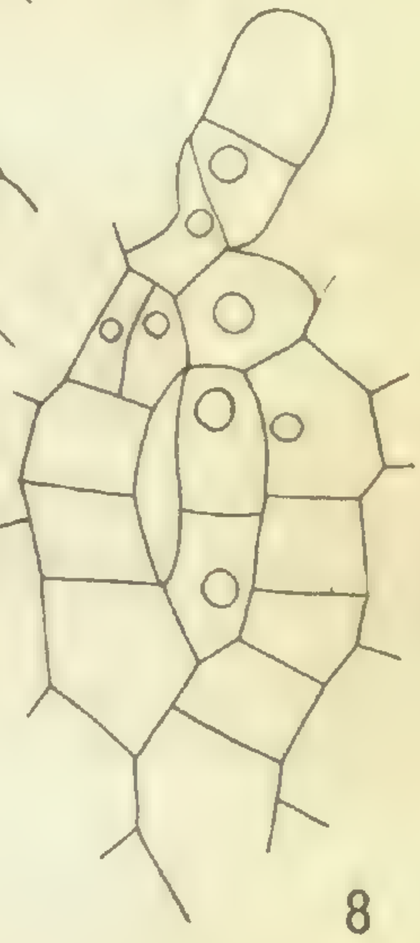

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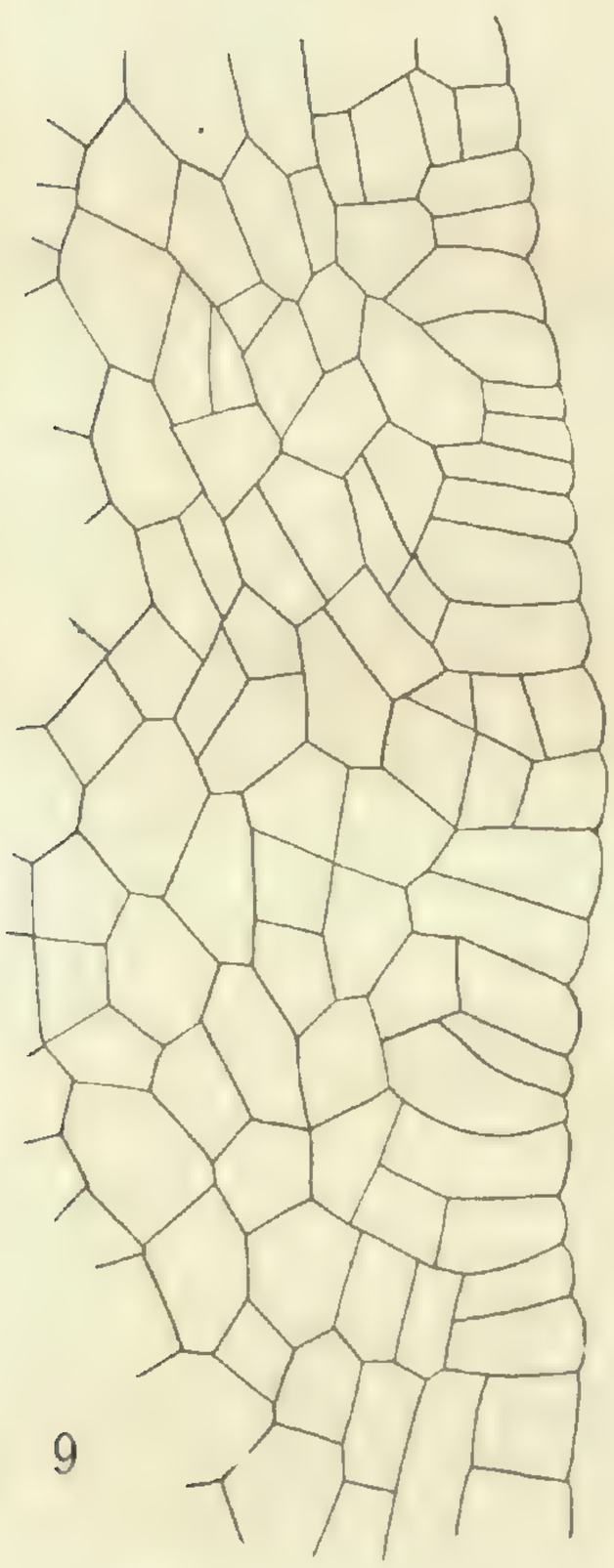

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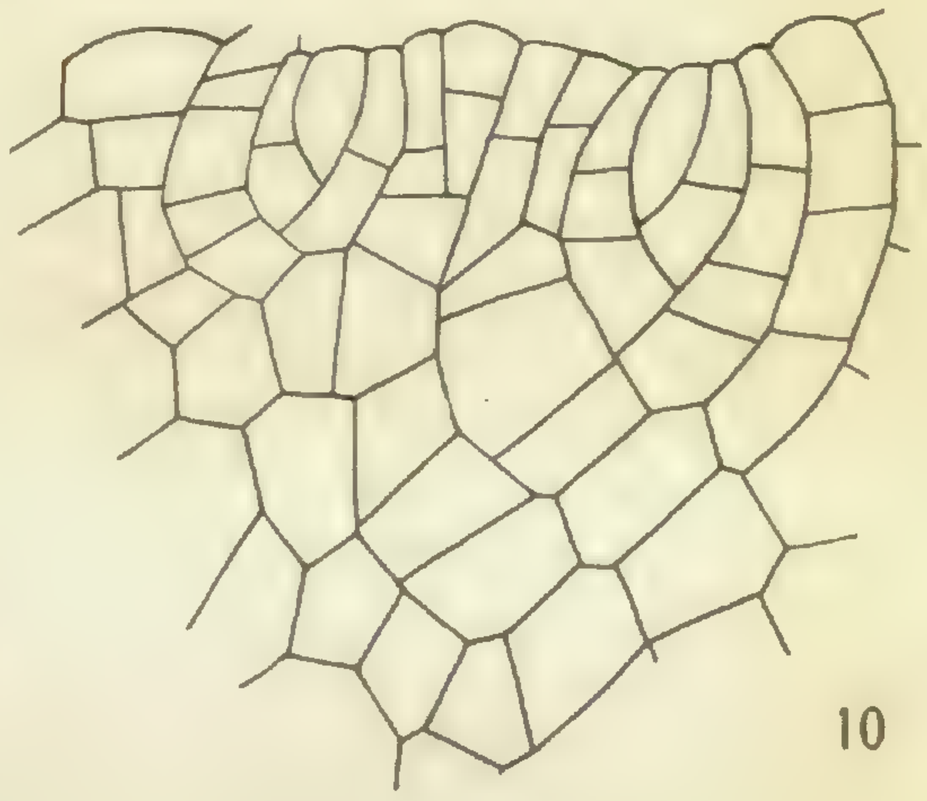

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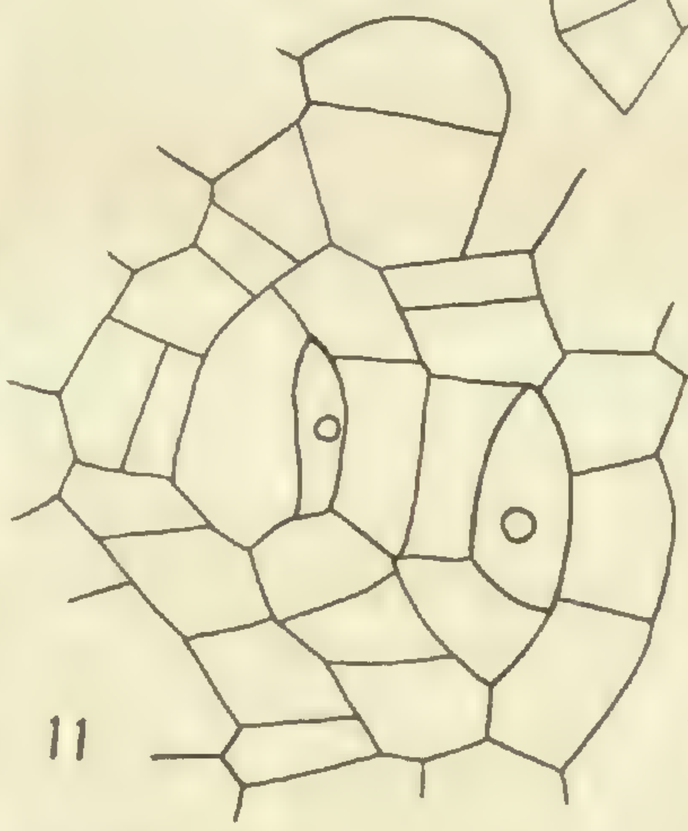

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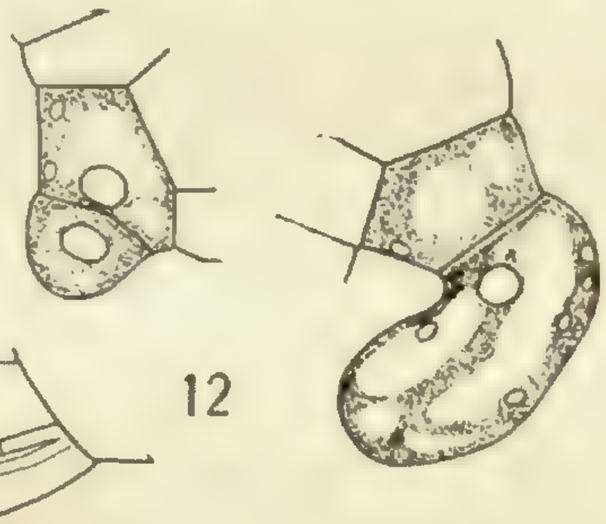

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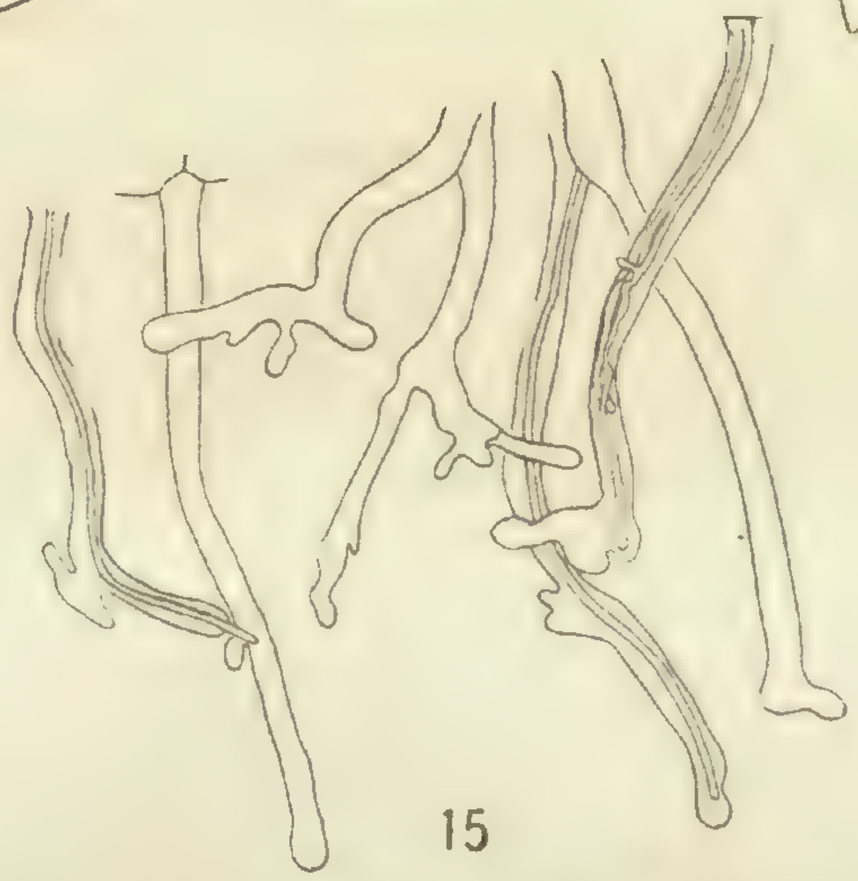

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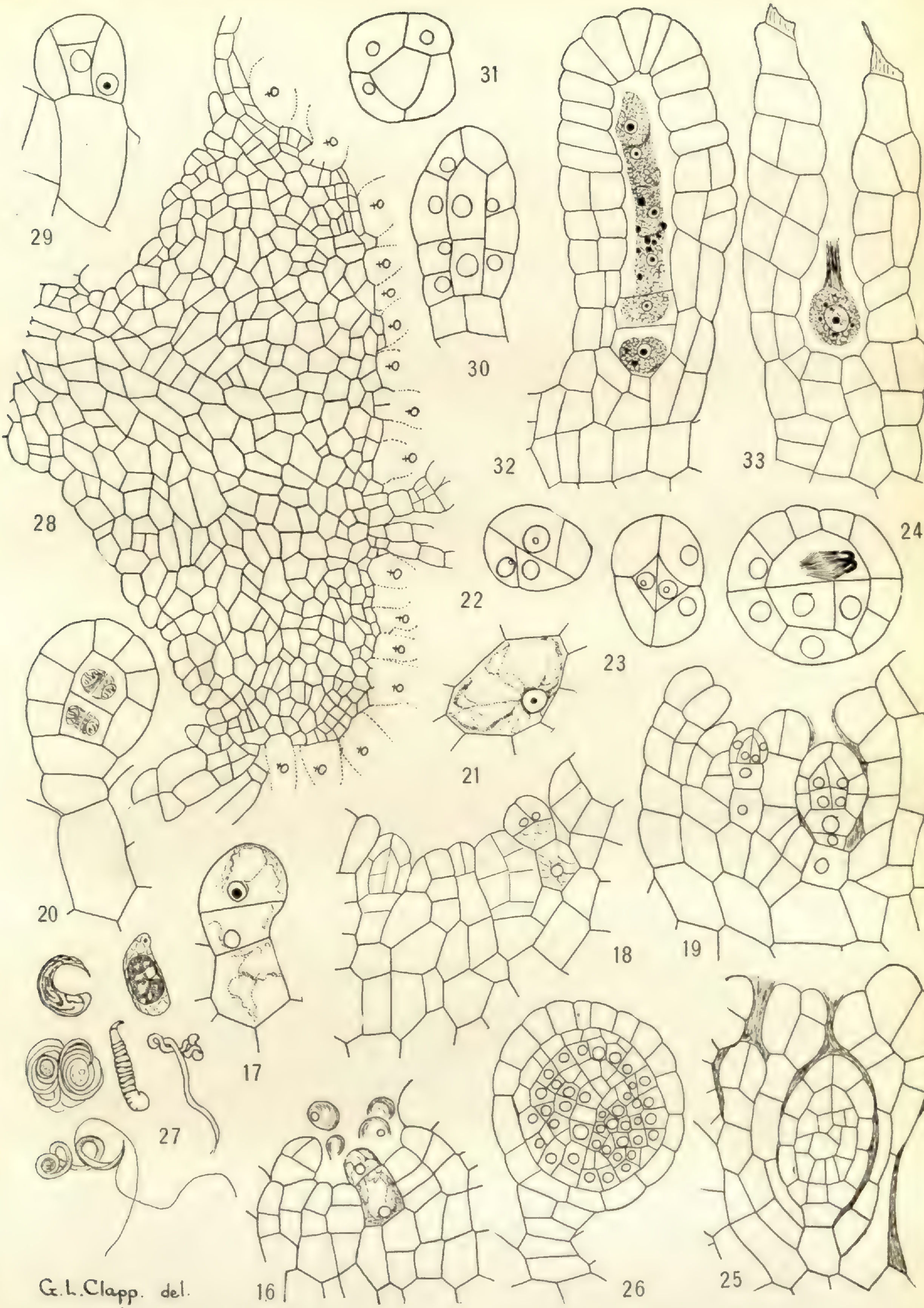

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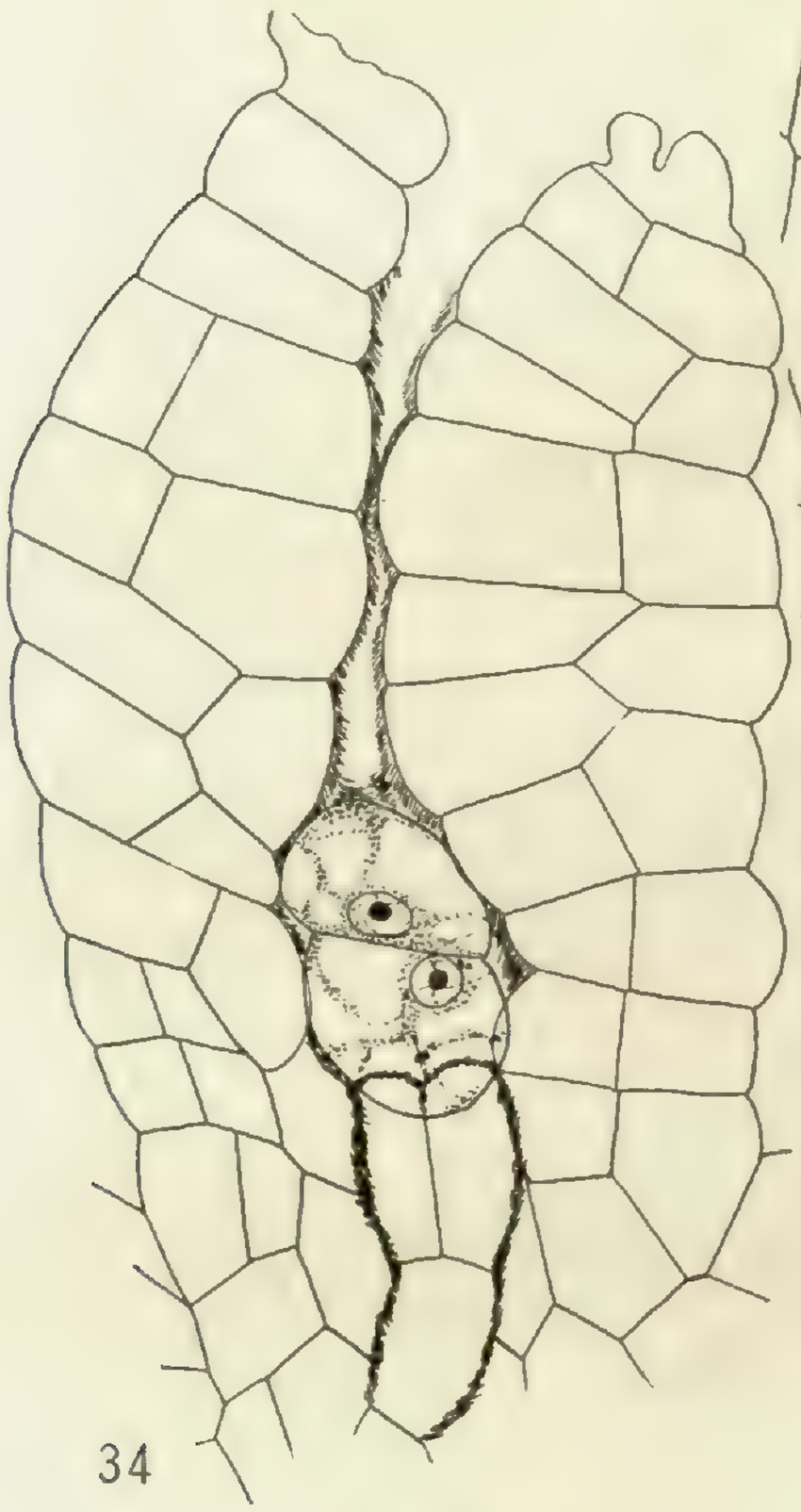

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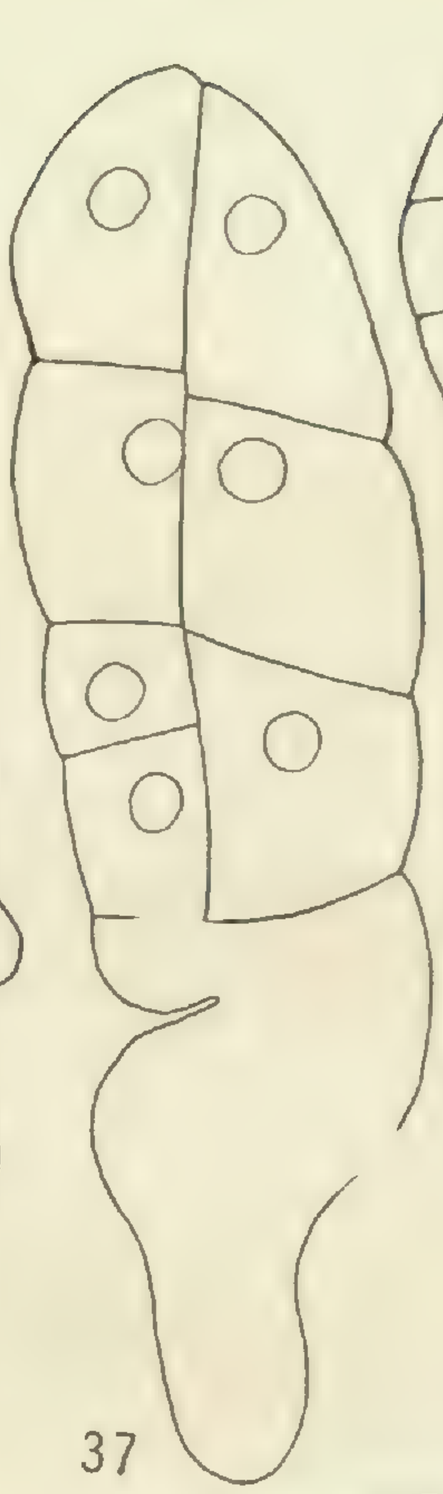

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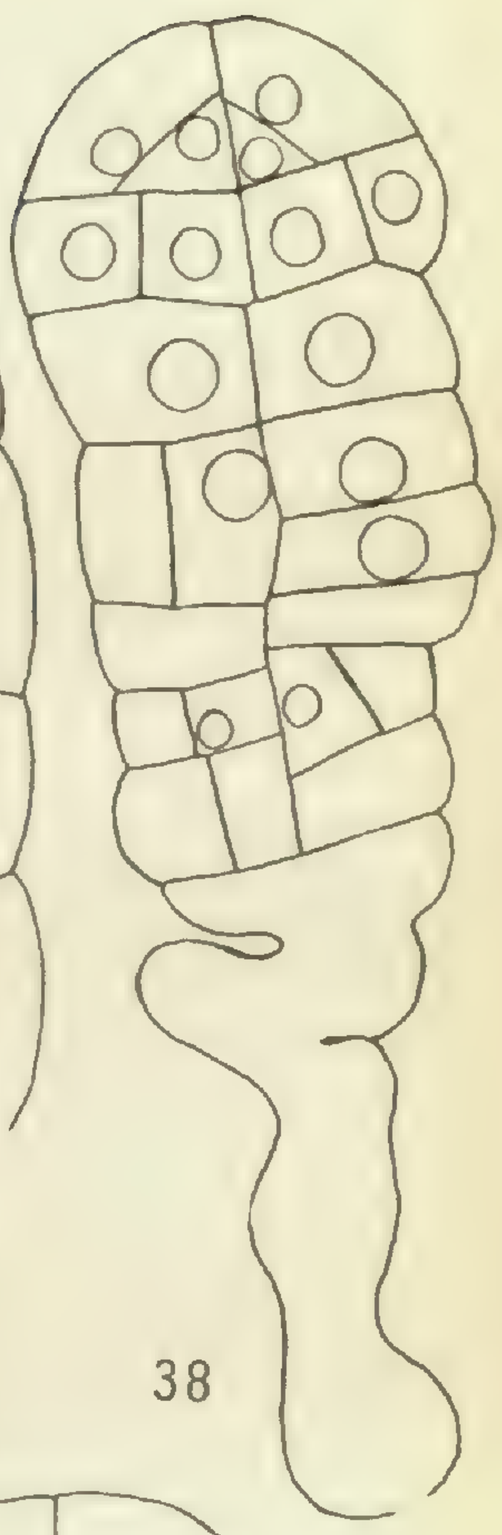

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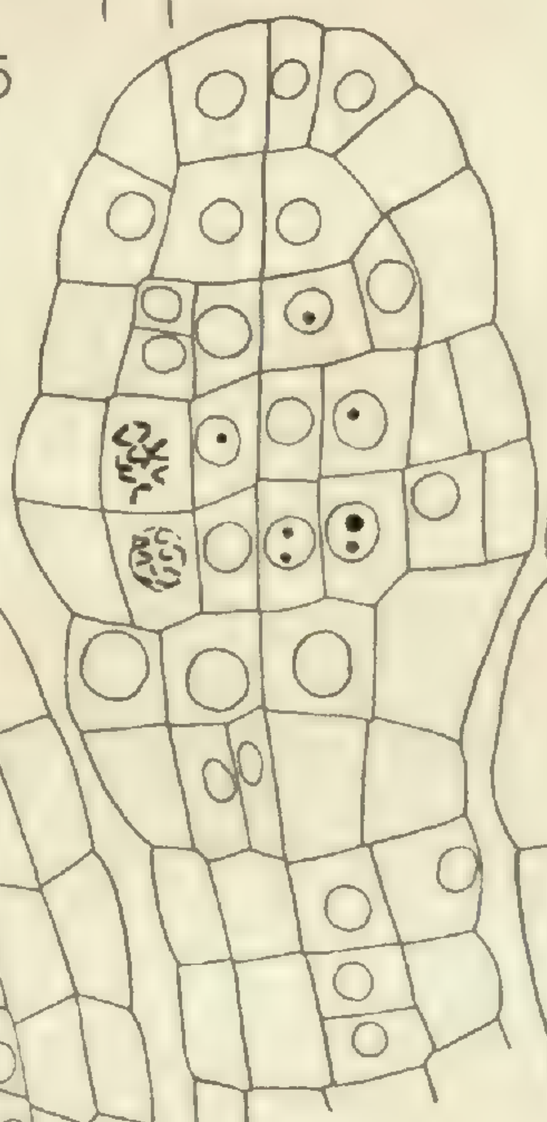

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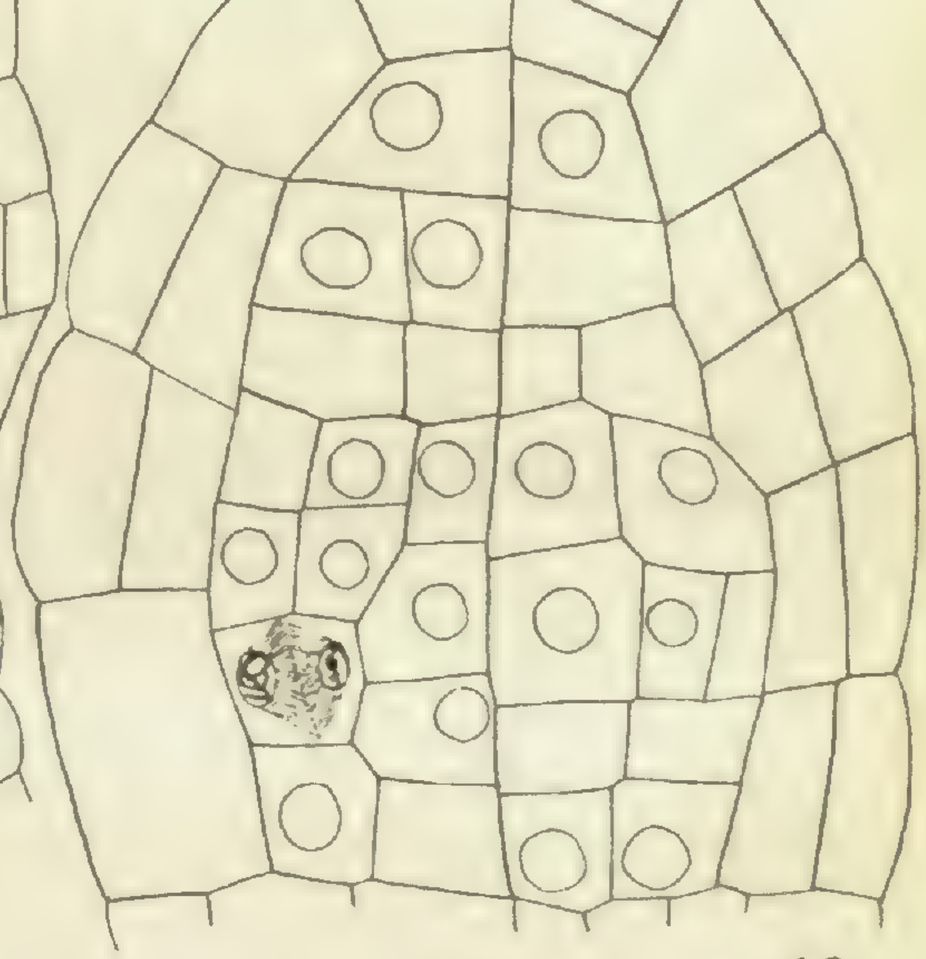

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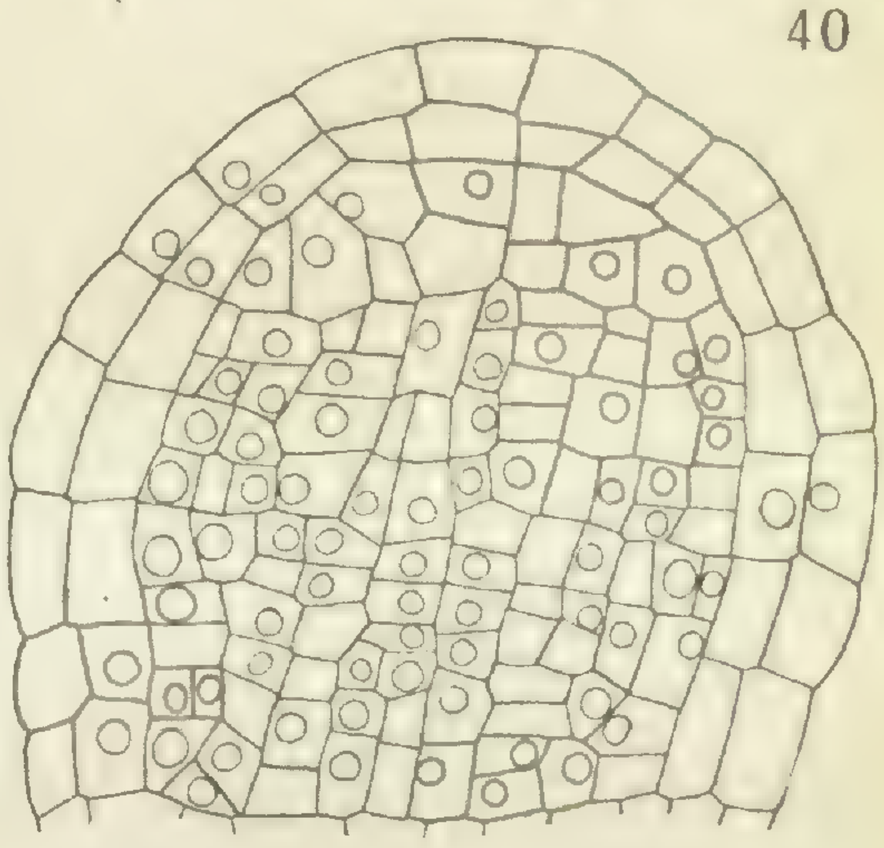

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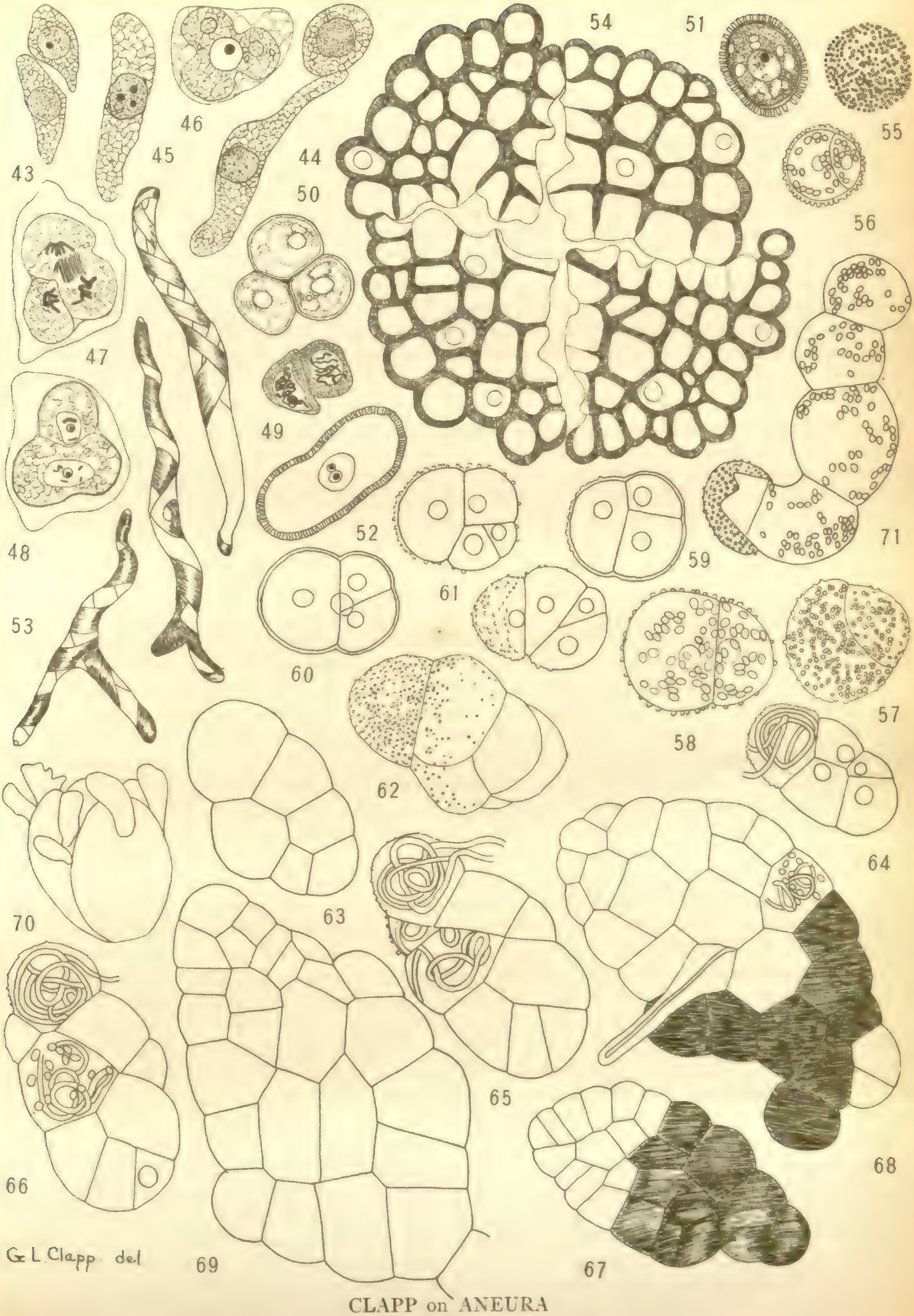
CLAPP on ANEURA



CLAPP on ANEURA

FIG. 38.—The primary wall layers and sporogenous tissue differentiated; ×1040.

FIGS. 39, 40.—Older stages of the sporophyte; the cushion of sterile cells and sporogenous tissue differentiated; ×1040.

FIG. 41.—Older sporophyte showing the meristematic region of the sporogenous tissue; ×505.

FIG. 42.—Delineation of elaterophore beginning; ×505.

FIGS. 43–50.—Young elaters and spore mother cells; ×1650.

FIG. 51.—Mature spore; ×1650.

FIG. 52.—Occasional form of mature spore; ×1650.

FIG. 53.—Branched elaters; ×830.

FIG. 54.—Cross-section of capsule, showing lines of dehiscence; ×830.

FIG. 55.—Germinating spore, swollen; ×830.

FIG. 56.—First stage of germination; ×830.

Figs. 57, 58.—The same stages a little later; ×1040.

FIGS. 59–63.—Stages in germination; spores developing on wet cotton; uninfected by fungi; ×830.

FIGS. 64–66.—Apical cell of thallus defined; fungus present; ×830.

FIGS. 67, 68.—Older thalli showing fungus present in darkened region; ×830.

FIG. 69.—One of the larger thalli, developed in capsule shown in fig. 70; ×830.

FIG. 70.—Capsule showing thalli from split valves; ×830.

FIG. 71.—Germinating spore without fungus; ×1040.

PLANT GEOGRAPHY OF NORTH CENTRAL NEW MEXICO[1]

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 160

J. R. WATSON

(WITH SEVEN FIGURES)

The area included in this investigation comprises the northern half of New Mexico, the most detailed study having been made of Bernalillo and portions of the adjoining counties containing a section of the Rio Grande Valley and the Sandia Mountains, but the results have been confirmed by excursions to other portions of the northern half of the territory.

The 35th parallel passes through the region under consideration, which indicates a hot sun during the summer and a warm one during the winter. The altitude ranges from a little less than 5000 ft. in the valley of the Rio Grande to about 11,000 ft. on the northern part of the Sandia Range.

The topography is varied. The recent valley of the Rio Grande, occupying the center of our region, is two or three miles wide. The floor is composed of beds of a hard clay ("adobe"), sand, and gravel. The water level is here usually only a foot or two below the surface and near the river often rises above it, leaving, when the water evaporates, a crust of alkali which whitens the ground like hoar frost on a November morning. The river is a shallow, muddy stream with a fall of five feet per mile. It may be a half-mile or more wide during the June melting of the snow on the Colorado mountains, or entirely dry during August, under the combined influence of drought and the demands of the irrigation ditches above. At low water it exposes extensive mud flats on which a vigorous plant growth quickly develops.

On either side this recent valley is limited by the much dissected edge of the mesa, which rises 100–300 ft. in a mile or two. These hills, although known locally as "sand hills," may be com-

[1] This study was undertaken under the direction of Dr. HENRY C. COWLES.

posed of sand, hard adobe, or a clayey gravel with stones up to the size of a man's head thickly strewn over the surface; or, more usually, all of these deposited in alternate layers, showing plainly its fluviatile origin. On the west side of the valley are occasional sand dunes bearing absolutely no vegetation.

From these hills a clinoplain, known locally as "the mesa" (not a true mesa), slopes gradually upward toward the mountains with a quite uniform grade of nearly 100 ft. to the mile, although appearing to the eye to be nearly level or gently undulating. This mesa is also of stream origin, consisting of the ancient gravels and clays of the Rio Grande intermixed with sand fans and other detritus resulting from the weathering of the mountains. On the east this plain stretches for nine or ten miles to the base of the Sandia Mountains, forming one of those old western river valleys so admirably described by MacDougal.[2] Every two or three miles this mesa is crossed by a sandy "arroyo," or dry stream bed, which once or twice each summer becomes a raging torrent for an hour or two. These arroyos lie in shallow valleys, the largest, however, having banks 100 ft. or more high. Few of these arroyos reach the river proper, but spread their flood waters over the floor of the recent valley, building up fans of an alluvium-like clay at their mouths. Numerous smaller arroyos head on the "mesa" proper or on its dissected edge. A similar mesa on the west side of the valley is partly covered by a flow of lava so recent that it has suffered almost no weathering, the shallow soil that covers it, to the depth of a few inches, having been deposited by the wind. A mile or so back from its edge this lava field is surmounted by five volcanic cones, the largest being about 300 ft. high.

From the eastern mesa the Sandia and Manzano mountains rise rather abruptly, sand and gravel fans at the mouths of the cañons forming a transition. The range is a typical block mountain with the principal fault at its western edge. It is composed of Archean granites and schists, capped by a layer of Carboniferous limestone 50–200 ft. in thickness. This limestone shows a dip to the southeast of about 20°. To the east of the main ridge lie

[2] MacDougal, D. T., Botanical features of North American deserts. 1908.

mountains of less elevation and Permian beds of red clay. Ten miles east of the Sandia Mountains the Ortiz and San Pedro mountains rise to an altitude of 8000 ft., followed by the fertile prairies of the Estancia Valley.

Climate

The most important factor in the climate is aridity. The precipitation at Albuquerque averages 7.43 in. per year; that of the mountains is much greater, but unfortunately has never been measured. Perhaps 20–24 in. would be a fair approximation for the higher parts of the range. The distribution of the rainfall is also an important factor. At Albuquerque the average for ten years was as follows:[3]

Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
0.48	0.33	0.22	0.26	0.69	0.35	1.43	1.07	1.7	0.77	0.46	0.31

It will be noticed that there is a rainy season beginning in July and one of less intensity in May. This is valuable to vegetation, as the bulk of the precipitation comes during the warm season.

It would appear from observation that a precipitation of less than 0.25 in. has no effect on vegetation, with the possible exception of some of the shallow-rooted grasses, as it does not penetrate the thirsty soil to a sufficient depth to reach the roots. On the other hand, much of the summer rain comes down in such a deluge that a goodly percentage runs off the mesa and especially its foothills. The distribution and the amount are both highly variable and materially influence the aspect of the vegetation from year to year. The May rains especially often fail altogether, and it is said that during a recent drought Albuquerque received not a drop of rain for thirteen months.

The distribution of the precipitation in the mountains is radically different. Judging from observation, the summer rains are about 50 per cent in excess of those at Albuquerque. But while snow is rare in the valley, the higher parts of the mountains are covered with it for a considerable part of the winter, and snowstorms frequently occur over the whole of the range and extend down some distance on the mesa. This snow, slowly melting,

[3] MAGNUSSON, C. EDW., Bull. Univ. N.M. no. 5.

thoroughly saturates the soil; much more so than the often torrential rains of the summer which quickly run off. The writer has been surprised to observe how brief an influence these summer rains have on the mountain streams and springs. A day or two after a heavy shower they are nearly as low as before, although they may have poured out a deluge for an hour or two. A heavy winter snow, on the contrary, maintains a steady flow throughout most of the summer.

TEMPERATURE

Because of its altitude and southern latitude, the climate is characterized by a comparatively low mean annual range of temperature and a high daily range. Although the thermometer is known to go to zero or below at night, the mean for January is 34° F. (MAGNUSSON, *loc. cit.*). This is due to the high temperature in the middle of the day (average maximum 46°). For July the mean is 76.4° F., the average maximum 89°,[4] and the average minimum 63.5°. The absolute maximum for the ten years was 104° F., and it has exceeded 100° F. on three different occasions. It is the occasional low temperatures which render it impossible for the larger, thicker cacti and century plants, so characteristic of southern Arizona and Mexico, to grow here. They have been planted repeatedly on the campus of the University of New Mexico, only to perish during the winter.

EVAPORATION FROM A FREE WATER SURFACE

The following data (MAGNUSSON, *loc. cit.*), giving evaporation in inches, show that the ratio of evaporation to rainfall is more than 10 to 1:

Jan.	Feb.	Mch.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
2.04	2.63	6.17	6.82	10.08	12.63	11.78	10.21	8.00	4.38	1.73	1.4

Total for the year 77.87 inches.

SOIL MOISTURE

Measurements of soil moisture gave the following results: sandy soil in the valley in December (dry season) 0.8 in. below the surface, 30 per cent; sandy soil in the "highlands" (edge of the

[4] A striking characteristic of the arid southwest is the great difference in temperature in the sun and in the shade.

valley), 1.9 per cent; sandy clay on the mesa, 3.9–10 per cent; sandy clay in May on the mesa, 4.8–7.2 per cent.

CAPACITY FOR HOLDING MOISTURE

Some determinations were made to determine the capacity for holding moisture, following the method used by LIVINGSTON,[5] with the following results. In the first column is shown the per cent of water absorbed in proportion to the dry weight of the soil; while in the second column the per cent of water is calculated in terms of "wet volume," that is, the volume of the dirt when allowed to settle under water. There is practically no humus in any of the mesa soil. In the piñon association there is a little humus, in the yellow pine association more, while in the Douglas spruce there is abundant humus.

Open mesa (Gutierrezia association)	23.8 per cent	37.3 per cent
Bigelovia association (edge of mesa) where		
Bigelovia was most luxuriant	21.4	35.4
Hymenatherum society of the association	12.7	25.8

WIND

A factor influencing the evaporation from plants is wind. Although the average velocity is probably not great, autumn and early winter being especially calm, there occur, especially in late winter and spring, violent windstorms which pick up the sand and even pieces of gravel large enough to break the glasses of a man walking against it. These violent winds plants must encounter, and this may be the factor which prevents the growth of lichens on the rocks on the mesa. The prevailing direction of the wind is south and southwest. This seems to be the explanation of the presence of sand dunes on the western edge of the valley and their absence on the eastern side.

LIGHT

In this clear atmosphere the illumination is of course intense and very annoying to the traveler in summer. Concerning the percentage of cloudiness MAGNUSSON presents the following aver-

[5] LIVINGSTON, B. E., Relation of desert plants to soil moisture. BOT. GAZ. **50**: 241–256. 1910.

age for ten years: days entirely clear, 219.4; days partly clear, 104.9; days cloudy, 38.4.

Plant formations and associations

Floristically the country is very interesting, as it is the meeting place of the northern and eastern flora with that of the arid southwest. On the slopes of the mountains the botanist familiar with the flora of the east would be able to recognize at least the genus of nearly every plant encountered, while upon the mesa, with the exception of *Gaura* and *Salsola*, scarcely a genus would be familiar.

RIVER VALLEY FORMATIONS

1. *Cottonwood forest*

Along the Rio Grande, where the water-table is never very far from the surface, there occurs an open and more or less pure forest of *Populus Wislizenii*. The trees are small, due probably to the operations of the native ranchers in their search for fuel and fence posts, for individual trees of this species planted in dooryards are veritable giants in girth. Scattered throughout this forest and especially along the banks of the streams are a few willows, clumps of the shrubs *Baccharis Wrightii* and *Cassia bauhinioides*, while on the ground grow *Juncus balticus*, *Trifolium Rydbergii*, *Aster spinosus*, and a little grass. This forest is monotonously uniform and poor in species.

2. *Juncus-Houttuynia association*

Alternating with the last in its possession of the river banks is a meadow-like association of which *Juncus balticus* and *Houttuynia californica* are the dominant plants. Just what factors determine which of these two associations will take possession of a given area is not clear to the writer. However, it would seem that, given time enough, the cottonwoods will occupy most of the situations. The *Juncus-Houttuynia* association, however, is not a necessary stage in the formation of a cottonwood forest, as the latter may develop directly from a mud bank. Whenever a mud bank is exposed for a few weeks in summer, a vigorous growth at once appears, of which young cottonwoods, willows, cat-tails, and

cockleburs are the dominant species. If one looks closely, many small annuals and numerous specimens of *Riccia fluitans* are seen; but one misses the bulrushes and sedges he would find in similar places in the east. The usual fate of such young growth is to be washed away upon the return of high water, but should this fail to happen for a year or so, the young cottonwoods may be large enough to hold the soil, and a forest develops. Other characteristic plants of this association are *Baccharis Wrightii*, *Helianthus annuus*, *Dysodia papposa*, *Onagra Jamesii*, *Amorpha fruticosa*, and *Rumex Berlandieri*. In more sandy places one meets *Aster spinosus*, *Maurandia Wislizenii*, *Sesuvium sessile*, and *Cycloloma atriplicifolia*.

Much of the valley is under ditch and as a consequence does not show the characteristic vegetation, but along the ditches a dense thicket usually develops, composed of *Cassia*, willows, sunflowers, *Solidago canadensis* var. *arizonica*, and others.

3. *Bigelovia association*

On higher ground, where the water level is deeper, there is found a variety of edaphic plant associations due chiefly to differences in slope and soil and the consequent ability to hold water. But on much of this area the dominant plant is *Chrysothamnus* (*Bigelovia*) *Bigelovii*, a low shrubby perennial, almost leafless, but the green shoots retain their color throughout the year, so that in winter, when the prevailing color of the landscape is brown, this formation may be detected ten miles away. It covers most of the higher gravel beds of the valley and the dissected border of the mesa, but stops abruptly and completely at the edge of the more level mesa. With the exception of the rock surfaces of the mountains, this is the most xerophytic of all our situations; the steep clay hills quickly shed what little water falls on them. In sandy places *Yucca glauca* is fully as abundant as the *Bigelovia*, and in places where a foot or two of sand covers a stratum of adobe, the *Yucca* becomes the dominant plant. In places where the sand is deep and extensive, such as the wider valleys or arroyos, a society, of which *Parosela* (*Dalea*) *scoparia* is the abundant plant, takes possession of the soil, often to the entire exclusion of *Bigelovia*, but not

of *Yucca*. This plant has slender wandlike branches which are regularly winter-killed for several inches. Other plants very abundant here are *Croton texensis*, the spiny ragweed (*Franseria acanthicarpa*), *Orobanche multiflora*, and *Cenchrus tribuloides*.

The steeper hills of this formation are too xerophytic even for *Bigelovia*, and here the low shrubby composite *Hymenatherum acerosum* is the most abundant plant. Associated with it usually are *Crassina* (*Zinnia*) *grandiflora*, *Ephedra trifurca*, whose leafless stems both look and feel like a branched *Equisetum*, and several species of *Eriogonum*. The *Crassina* has a method of seed dispersal that is not mentioned in any text with which I am familiar. The very large ligules of its ray flowers, instead of dropping off, become dry and papery, and when the seeds are ripe, the whole head separates from the stem and goes rolling off over the plain and hills, a diminutive tumbleweed.

The arroyos of this dissected edge of the mesa show an interesting succession of societies, characterized by successively smaller plants as one ascends. If sufficiently large to deposit considerable sand, their lower courses are occupied by the desert willow (*Chilopsis saligna*), a plant with pretty *Catalpa*-like blossoms. Its leaves, however, resemble very closely those of such a willow as *Salix longifolia*. It is the tallest shrub outside of the mountains and the cottonwood forest, reaching a height of 15–20 ft.

Ascending the arroyo this society is replaced by one in which *Fallugia paradoxa* is dominant. This rosaceous plant is very slow to drop its leaves, retaining them until late in the winter. It has pure white blossoms and plumose fruit. It grows to a height of 3–4 ft. in dense thickets, which are even more dense underground, where about half of the stems are found, in which respect it resembles the famous mesquite of more southern regions, the plant which gave rise to the expression that in New Mexico one "climbs for water and digs for wood." Here grow also two low perennial evergreen composites, *Berlandiera lyrata* and *Melampodium cinereum*. After the summer rains there appears here, as on the mesa, a relatively abundant growth of annuals, among which the composites *Hymenopappus flavescens*, *Thelesperma gracile*, and *Baileya multiradiata*, together with *Pentstemon ambiguus*, are characteristic.

A little higher up, where the arroyo is not over 6–8 ft. wide, the bed proper is generally free from plants except an occasional *Euphorbia*, but the banks are occupied by *Bigelovia*. Near its head, where the arroyo is only 1–2 ft. wide, its sides are occupied by a narrow fringe of shrubs, chief of which are *Parosela formosa* and *Lycium pallidum*.

In the valleys of the larger arroyos that continue the mountain streams there appears yet another society, characterized by the dominance of either *Suaeda Moquinii*, or the greasewood *Sarcobatus vermiculatus*, or both, the former being more particularly confined to the adobe fans at the mouths of the arroyos. Like so many of the shrubby plants of this region, these and especially the *Suaeda* catch the wind-blown dust and allow it to accumulate among its stems, making mounds like low sand dunes, but in this case composed of adobe. For this reason this association is covered with hummocks often 6 and sometimes 10 ft. high. This is an alkali society, due to the evaporation of the flood waters of the arroyo, and has the same relation to the arroyos as a floodplain forest to a river valley in the east. Mixed with salt grass it is the dominant association around the salt beds and lakes of the Estancia Valley, as well as along the Rio Salada branch of the Jemez River.

MESA FORMATION

This occupies the more level ground of the mesa proper and stops abruptly at its dissected edge, as stated under the last heading. This was undoubtedly originally a grassland, and is so yet where it has not been too seriously over-grazed. It should probably be classified as a steppe. Now, thanks to lack of scientific control of grazing, it has been so invaded by the composite *Gutierrezia* (a somewhat shrubby perennial that grows to be 3 ft. high, and is often called "goldenrod") as to merit being called a *Gutierrezia* formation (fig. 1). The seasons of 1909 and 1910 were drier than usual until about July 20, and as a result 90 per cent of the plants are entirely dead and most of the remainder show only a small branch or two alive. In the autumn of 1907, after an unusually wet (or less dry) season, the entire mesa was a sea of gold, but during those two years it bloomed only in the mountains and

along trails where there is less crowding and where the dust of the trail conserves the moisture after the principle of dry-farming. In 1911 the summer rains commenced in late June and the plants that survived are thrifty and show abundant bloom.

The mesa is monotonously uniform, especially in winter when one may ride for miles and see only a few grasses, *Gutierrezia*, clumps of *Opuntia fragilis*, or occasionally a *Yucca glauca* or a prickly pear (*Opuntia* sp.).

FIG. 1.—The head of an arroyo on the edge of the mesa: in the foreground, *Gutierrezia*, *Salsola*, and *Yucca glauca;* to the extreme left a clump of *Chrysothamnus Bigelovii;* in the distance the *Gutierrezia* association.

The plants of the mesa belong to three ecological groups. (1) Plants like the cacti, *Bigelovia*, *Yucca*, *Sarcobatus*, and *Suaeda*, which have large, usually underground stems or roots, in which moisture is accumulated. (2) Annuals and perennials with underground stems, including by far the largest number of individuals, but usually not the largest and most conspicuous. They are plants which are able to wait for the rains and then to make an exceedingly rapid growth and maturity. Here belong most of the mesa herbs and grasses. The latter cure perfectly *in situ* and make most excellent hay. It is this property of the grasses that makes the grazing industry possible in this country. (3) The third class includes a few plants that are winter annuals. The

fall rains and the occasional snow flurries during the winter afford them sufficient water for growth in favorable situations, and they are ready to blossom with the spring rains. The most conspicuous examples in this class are *Phacelia corrugata*, some of the loco weeds (*Astragulus* sp.), *Draba*, *Gilia*, and sometimes *Gaura coccinea*, *Sideranthus spinulosus*, and many of the plants that are ordinarily summer annuals may occasionally develop during the winter and blossom with the first shower of spring or summer. Indeed, the one feature of the vegetation of this region that attracts the attention of one accustomed to more humid regions is the absence of seasonal periodicity on the part of most of the herbs and many of the shrubs. With regard to relatively few species can one speak of spring, summer, and autumn flowers here. They grow and blossom when the rains come, be that March or August. During 1909 and 1910 the rains came July 20 and July 23 respectively, and the result was that the mesa was brown and lifeless until then, but by August 1 it was a garden, nearly covered by a mat of vegetation, made up of grasses, *Abronia*, *Allionia*, *Townsendia strigosa*, *Houstonia humifusa*, *Plantago Purshii*, *Asclepias brachystephana*, *Wedelia incarnata*, Russian thistle, and *Solanum elaeagnifolium*. By September 10 all was over and the mesa had assumed its usual brown hue. Thus in six weeks the annuals and the underground perennials had grown, flowered, and matured their seeds. The exceptions to this rule are those plants in the first class, the larger shrubs, the cacti, yuccas, and other plants having thick roots or stems providing for the storage of water. With May come the blossoms of the stemless evening primroses (*Oenothera* sp.), the chimaja (*Cymopterus*), and the wild onions. When June arrives, we have the flowers of the cacti, yuccas, and the desert willow; while September brings out the blossoms of *Bigelovia* and October the *Gutierrezia*, if there has been rain. This formation and the next two are classed as Upper Sonoran by MERRIAM and his followers.

In the middle of the mesa, 15 miles to the south, the outcropping of a layer of sandstone causes a succession of springs to appear, and about these springs are cottonwoods, *Juncus*, *Houttuynia*, and other plants of the valley. In other words, a spring changes Upper

Sonoran to Lower at once. On the other hand, there appears on the rock cedars and other plants characteristic of the next formation. This association is also spread over the mesa west of the river and over the lava field where the species are identical with those of the sandy clay of the mesa, but some, especially *Gutierrezia*, are stunted. Here also are a few cedars, *Rhus*, and other mountain plants. This lava field seems to receive slightly more rainfall.

As one approaches the mountains and ascends one of the sand or gravel fans at the mouths of the cañons, a new plant appears,

FIG. 2.—At the base of the Sandia Mountains: *Opuntia arborescens* society; *Rhus trifoliata* appears in the center, and in the background on the rocky slope are black looking clumps of *Nolina*.

Opuntia arborescens, whose cylindrical stems, 6–8 ft. tall, bear beautiful deep rose blossoms in June, and yellow fruit the remainder of the year (figs. 2 and 3). These cacti form dense thickets, which with *Yucca glauca*, *Croton texensis*, and *Fallugia*, which again become abundant here, are quite as characteristic features of these fans as the more abundant *Gutierrezia* and grasses.

CEDAR FORMATION

Next comes the formation of which *Juniperus monosperma* is the dominant plant. East of Albuquerque it is confined strictly

to the mountains, but where the mesa rises higher (6500 ft. or over) it stretches out over the plains. In the Estancia Valley it seems to be spreading at the expense of the prairie, as considerable areas are dotted over with young trees where there are no signs of old ones. But in many places, as here, it clings to the rock outcrop and to the neighborhood of scattered rocks, doubtless because of the moisture conserved under them. In this connection it is

FIG. 3.—*Opuntia arborescens* in fruit: to the left is an arroyo

interesting to recall the occasional occurrence of cedars on the lava a thousand feet lower. That the lower edge of this formation is limited by the supply of soil moisture is evident. On the whole, it coincides quite closely with the lower limit of the usual winter snow. Near the lower edge, especially, the trees are far apart, broken, stunted, gnarled, constantly recalling an old neglected orchard in a back pasture in Ohio. *Gutierrezia* and *Yucca glauca* extend into this formation and *Opuntia arborescens* is abundant

and characteristic. Other members are *Rhus trilobata*, *Nolina texana* (a long-leaved liliaceous evergreen), and the spiny-leaved oak, *Quercus undulatus*. The *Rhus* is also imperfectly evergreen, and indeed there is less difference between the winter and the summer aspect of this formation than of any other, because there is less difference in the relative humidity of the soil.[6]

PIÑON FORMATION

This has been combined with the last by MERRIAM and other writers, and they do shade into each other very gradually, even imperceptibly, but no more so than do the *Pinus ponderosa* and Douglas spruce formations, which are separated by these authors. Furthermore, the piñon (*Pinus edulis*) never extends as far down the mountain side as does the cedar, the differences being on the average at least 500 ft. Other plants very characteristic here are *Yucca baccata* or "amole," mountain mahogany (*Cercocarpus parvifolius*), *Philadelphus microphyllus*, *Lesquerella Engelmanni*, and *Tragia nepetaefolia*.

YELLOW PINE ASSOCIATION

This is the "transition zone" of MERRIAM, which he states is on the whole more closely related to the Sonoran than to the Boreal, a conclusion which seems to the writer to be incorrect at least so far as plants and insects are concerned. The latter are treated in another publication.[7] The characteristic plants, after the *Pinus ponderosa scopulorum*, are *Geranium atropurpureum*, white oaks, red cedar (*Juniperus scopulorum*), the pasque flower (*Anemone patens Nuttalliana*), wild gooseberry (*Ribes divaricatum irriguum*), *Ptelea mollis*, wild grape (*Vitis arizonica*), cudweed (*Antennaria plantaginifolia*), and New Jersey tea (*Ceanothus Fendleri*). Here occurs a sharp and complete change of flora. There is much more difference between this formation (fig. 4) and the mesa or even the piñon formation less than a mile away, than there is between it and the woods of Ohio, as witness the preceding genera, if not species.

[6] Whether the oaks and *Rhus* drop their leaves early in the winter or carry them until spring is determined by the soil moisture. In less dry winters and along arroyos they retain them. Under more xerophytic circumstances the leaves are dropped.

[7] Report of the N.M. Resource and Conservation Commission. December 1911.

Here is a most interesting tension line between the flora of the arid southwest and the more humid north.

The association descends in some places to 7000 ft., and extends to the top of the range at 10,000 ft., and coincides very closely with the region of deep winter snow. On the western slope its aspect is somewhat different from that of the eastern slope. On the

FIG. 4.—View toward the south in the Sandia Mountains (about 8500 ft.) in the yellow pine association: in the foreground the oak chaparral (*Quercus* sp. and *Robinia neo-mexicana*) and yellow pine, and to left of center a Douglas spruce; in the distance, covering a north-facing slope, is the Douglas spruce association.

former it reaches its best development in amphitheater-like U-shaped valleys, which collect the winter snow and practically protect the trees from the drying winds and sun of summer. These areas I have called "pine parks." On the east slope, with its greater precipitation, the forests are more extensive and possess a flora which reminds one very forcibly of that of the pine forests of Kentucky, especially where there has been a fire. The dominant

grasses here, as there, are species of *Andropogon*, and mixed with them are *Liatris punctata*, *Ratibida columnaris pulcherrima*, and *Zygadenus*.

In places along streams charged with lime the red cedar often takes almost entire possession of the soil, forming a quite distinct association.

FIG. 5.—Top of Sandia Mountains: white oaks occupying a depression where they are sheltered from wind.

In the Sandia Mountains the white oaks are very characteristic of this formation, but in the more mesophytic Jemez Mountains, and also on Mt. Taylor, where the yellow pine grows even more luxuriantly, there is much less oak, and MERRIAM states that none was seen on the San Francisco Mountains, although COWLES reports its occurrence upon the southern slopes. The explanation of this varying amount of pine and oak is to be found in the fact that the oak is able to grow in more xerophytic situations than the pine (fig. 5). It, with *Robinia neo-mexicana* and bearberry

(*Symphoricarpus rotundifolius*), forms a dense and almost impenetrable chaparral 4–5 ft. high, which covers the highest, steepest slopes, and the wind-swept and therefore xerophytic mountain tops. In these parts of the range there is very little pine or spruce, except on north-facing slopes, and from a study of the Sandia Mountains alone one would be tempted to place the oaks in a separate formation; but there are clumps of oak among the pine in all situations, and the study of other ranges would seem to indicate that they belong to the same formation but that the oaks form a more xerophytic association in this formation. Furthermore, both the oaks and the locusts reach their maximum size only in the more mesophytic places among the pines and spruces.

The herbs of this association are also somewhat different. Conspicuous are several species of *Pentstemon*, *Campanula rotundifolia*, *Ceanothus Fendleri*, *Thalictrum Fendleri*, and somewhat less common are *Hedeoma Drummondii*, *Gentiana affinis*, and *Calochortus Gunnisonii*.

In the Manzano Mountains the alligator juniper is common in what is chiefly the *Pinus-Andropogon* association, but having some elements of the piñon formation. This would seem to be about the northern limit of *Juniperus pachyphloea*, as it is entirely absent from the Sandia Mountains.

Mountain meadows

In places (usually saddles) on the top of the range, the chaparral gives place to a meadow-like growth, composed, however, not chiefly of grasses, but of low herbs, *Potentilla*, *Castilleja*, *Brickellia*, *Chrysopsis villosa*, *Aphanostephus humilis*, *Gymnolomia multiflora*, *Actinella acaulis*, *Achillea lanosa*, *Oxytropis Lamberti*, *Allium stellatum*, and cacti of the genera *Mamillaria*, *Cereus*, and *Echinocactus*.

These open places are small, the largest being about a half-mile long, and they occupy the less xerophytic situations. They are sufficiently numerous to enable one to walk with comparative ease along the summit of the range, dodging from one to another and thus avoiding most of the chaparral.

DOUGLAS SPRUCE FORMATION

Covering north-facing slopes above 8000 ft. and extending down the narrower cañons to about 7000 ft., we have a formation of which the Douglas spruce (*Pseudotsuga taxifolia*) is the dominant tree (fig. 6). This is the most mesophytic and dense of all our forests. Here occur the blue and Canada violets, *Berberis aquifolium* (*repens*), *Galium* sp., *Monarda fistulosa*, *Mertensia oblongifolia*, *Polemonium foliosissimum*, *Pachystima myrsinites*, *Oxalis violacea*, *Prunus demissa*, *Fragaria*, *Rosa arkansana*, *Amelanchier alnifolia*, *Heuchera parvifolia*, *Sedum Wrightii*, *Corydalis aurea*, *Clematis* (*alpina*) *occidentalis*, *Aquilegia canadensis*, *Stellaria Jamesii*, and *Smilacina stellata*. This is the "Canadian zone" of MERRIAM, but nowhere in this locality does it make a complete belt around the mountains. It occurs in its full development only in the most mesophytic places, as in the narrower V-shaped cañons and on north-facing slopes where snow accumulates in huge drifts

FIG. 6.—In the cañon the Douglas spruce association; on the rocky slope the *Pinus ponderosa* association; in the foreground, white oaks, verbena (in bloom), and mountain mahogany; a small red cedar to the right of the rocks in the center.

during the winter, but scattering trees, dwarfed and stunted, rise from the chaparral over most of the summits of the range mixed with the yellow pine, especially at lower levels, and with the blue spruce (*Abies concolor*) at higher. On North Sandia Mountain, which, on account of its greater elevation and perhaps more east and west trend, has a higher precipitation, the latter tree forms almost pure forests. On the ground in its shade is a luxuriant and in places an almost pure growth of *Goodyera Menziesii*.

FIG. 7.—Top of North Sandia Mountain: *Picea Engelmannii;* in the foreground, *Potentilla*, *Castilleja*, and *Aphanostephus*.

On the very highest and most exposed part of North Mountain the first are replaced by Engelmann's spruce (fig. 7). This would place it in MERRIAM'S "Hudsonian zone," and it is so mapped. On these heights one meets an occasional *Pinus flexilis*.

CAÑON ASSOCIATIONS

Ascending a cañon a very interesting succession of associations presents itself. The first tree met approaching the mountains from one of the arroyos is the hackberry (*Celtis reticulata*), usually only a few scattered trees or a clump here and there. Next comes

a society dominated by box-elders, also rather scattered, and with considerable grape (*Vitis arizonica*). These seem to be the cañon representatives of the cedar and piñon formations respectively.

Higher up and in the narrower, more mesophytic portions of the cañon there occurs a society dominated by *Populus angustifolia*. This corresponds with the pine formation on the whole, and if the cañon is open or U-shaped, the yellow pine will occupy the floor with the poplar along the stream. Ascending still higher, where the cañon becomes decidedly V-shaped, the Douglas spruce formation holds full sway. And as one nears the head, above the permanent stream there usually occurs an association of quaking aspens, somewhat less mesophytic than the Douglas spruce formation. In the shade of the aspens grow *Rubus deliciosus*, *Osmorrhiza nuda*, *Saxifraga bronchialis*, *Jamesia americana*, *Delphinium scopulorum*, *Actaea spicata*, *Pedicularis procera*, *Frasera speciosa*, and nearly always young spruces. After a fire in the Douglas spruce the quaking aspen always takes possession, but it has also its natural place as a transition between the oak chaparral and the Douglas spruce in the biotic succession.

The biotic succession in the Sandia Mountains is as follows: the bare rock first incrusted with crustose lichens, then foliose lichens, mosses, herbs, oaks, followed in some cases directly by Douglas spruce and in others by aspen and then the spruce; and then as physiographic succession comes in, the poplars, pines, and box-elders in the cañon; and pine, piñon, and cedar on the slopes, until the ultimate formation of the mesa is reached.[8]

Response to climatic factors

This complex of associations is of course due to a complex of causes, of which the most important are relative humidity of the air and more especially that of the soil, and not the average temperature of the growing or any other season, as some eminent authorities have maintained. Temperature, of course, is a factor, but principally as it affects the humidity. I have mentioned the inability to grow certain cacti because of the winter's cold. There

[8] A study of Mt. Taylor indicates that the alligator juniper has a place between the yellow pine and the piñon.

are narrow cañons in the lower parts of the mountains which would doubtless be occupied by Douglas spruce were they situated at a greater elevation, chiefly because of the greater precipitation. On the other hand, most of the trees of the mountains are growing on the campus of the University of New Mexico at an elevation of only 5200 ft., but they are carefully irrigated, and the Douglas spruces are in the shade of cottonwoods. The storksbill (*Erodium cicutarium*) grows in the mountain cañons and at an elevation of 5000 ft. in the valley. In the former situations it is in blossom nearly all winter, often directly beside a snowbank, and doubtless because of the snowbank, while those in the valley do not bloom until the May or July rains.

Fallugia paradoxa is a most interesting plant in this regard. As mentioned above, it is a very characteristic plant in the arroyos of the mesa and its edge down to less than 5000 ft. It grows at a lower altitude than this farther south, and doubtless would here were there lower altitudes. Now these arroyos are the hottest places in this region. Their sands reflect the desert sun's glare and the banks obstruct the breeze. Yet this same *Fallugia* forms thickets on the Sandia Mountains at an elevation of over 9000 ft. on steep slopes facing the southwest, and it grows at all altitudes between. On a basis of temperature control, this distribution seems inexplicable. But these arroyos are the least xerophytic places on the mesa. The soil at the depth of a foot or two is always moist, due to the fact that the arroyo brings down a flood of water two or three times each summer and the sand conserves this and the rain most thoroughly. On the contrary, those steep southwestern slopes are the most xerophytic places in the mountains, with the exception of course of bare rock. But on account of greater rainfall, these most xerophytic places of the mountains are about as moist as the least xerophytic places on the mesa, and *Fallugia paradoxa* occupies both situations.

On an ascent of the mountains made on May 8, 1910, the oaks in the lower parts of the cañons were found in full leaf, and their blossoms gone; a little higher they were just leaving out and blossoming; at the top of the range not a bud had started. Again, on October 6 the leaves were still green and vigorous at the base,

but on the summit brown and frost-killed. Thus it is seen that the growing season is at least a month shorter on the summit, but the same oaks grow in both situations.

Another illustration of the influences of moisture is seen along the Jemez River. This fair-sized stream comes roaring down off the Jemez Plateau through a rather shallow cañon which faces the south. This (altitude 6000–7000 ft.) is occupied by the Douglas spruce formation, but the slopes on each side are occupied by piñon, the yellow pine being largely omitted. The branches of the spruce and piñon are in places at the same level and subject to the same hot sun and consequently the same temperature, but the roots of the Douglas spruces have access to the unfailing water supply of the stream.

This tendency of the "Canadian zone" to creep down the cañons and of the Sonoran to ascend the ridges is noted by MERRIAM, but is explained as due to warm and cool winds, vertical exposure to the sun, etc. It receives a much simpler explanation in that the ridges are more xerophytic than the cañons. At night, when a plant is supposed to make a goodly share of its growth, these ridges are little if any warmer than the adjacent cañons. They are subject to greater and more sudden changes of temperature, to drying winds, and are less able to hold their moisture—*they are more xerophytic*.[9]

In most situations in the Sandia Mountains the oaks of the transition zone entirely surround the colonies of the Douglas spruce (Canadian zone). In watching the Sandia Mountains during four winters I have been struck by the very close correlation between the lower limit of the average winter heavy snow and that of the lower limit of the yellow pine. I believe that it is chiefly these snows that determine the distribution of this tree. Far be it from me to maintain that the temperature has no effect on the plants of this region. I am simply contending that in this arid region, at least, water is more important. Any scheme for mapping "life zones" should be based on all the factors determining the same and not on one alone.

[9] This same tendency is seen in the Rio Grande Valley, where occur many eastern and northern genera and even species (as *Aster*, *Solidago*, *Cassia*, etc.) which are absent from the higher but drier mesa.

Light also is of course a factor even with the plants of the mesa. I tried to grow some *Yucca* and *Fallugia* in the slight shade of some box-elder trees, but they all died. It is probable that light is quite as important indirectly through its acceleration of transpiration as directly through its relation to photosynthesis.

Furthermore, these different factors may be of a very diverse importance in different groups. What may be an effective barrier for one form of life may have little influence on others. The sum total of heat during the season of reproduction may well be more of a barrier to mammals than to plants. BANKS has remarked in a recent publication that it would seem to be necessary to have a different arrangement of zones for at least every family of insects.

Summary

1. In North Central New Mexico the arid climate of the southwest meets (in the mountains) the more humid one of the north and east.

2. Corresponding with this abrupt change of climate there is an abrupt change of plant life.

3. The genera and some of the species of the mountains are identical with those of the east; those of the mesa are entirely different. There is a greater difference between the flora of the yellow pine association and that of the mesa, less than a mile away, than between the former and Ohio and probably even Europe or Japan.

4. The chief factor determining this change is moisture, the supply of which is largely determined by precipitation, ability to hold it, and protection from drying winds and sun, as shown by the following facts:

a) The same plants (*Fallugia*, *Erodium*, oaks) occur throughout a great range of altitude and temperature, but in soil of about the same degree of humidity.

b) Spruces and piñons will grow with their branches almost touching if the roots of the former have access to an unfailing water supply.

c) A spring will change "Upper Sonoran" to "Lower Sonoran."

d) Plants as *Erodium* or *Draba* bloom much earlier in the cooler but moister mountains than on the warm but arid plain.

e) A patch of mesophytic spruces ("Canadian zone") is very frequently entirely surrounded by the more xerophytic oaks of the "Transition zone."

f) The tendency of the higher zones to creep down the cañons and of the lower zones to creep up the ridges receives a much more plausible explanation in connection with the supply of moisture in the two situations, than through the cooling effects of descending currents and the warming effects of ascending ones.

5. An arrangement of "zones" should be based on all factors determining the distribution of life and not on one only, especially in a region where that one is of secondary importance.

6. Most of the plants of the mesa do not show the marked seasonal periodicity of the east.

7. Plants having large organs for the storage of moisture do show seasonal periodicity.

8. A characteristic of much of the vegetation is the ability to lie dormant until the rains come, and then to make an exceedingly rapid growth and reproduction.

9. The differences in amount and distribution of rainfall in different years causes a more marked response in plants (shown by height and reproductive activities) than in more humid regions.

10. The region is a particularly good one in which to study physiographic plant ecology because of the abrupt differences in physiography and climate.

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THE PERFECT STAGE OF ACTINONEMA ROSAE[1]

FREDERICK A. WOLF

(WITH PLATE XIII)

Perhaps no plant disease has been more widely observed or is more generally known, both in Europe and the United States, than the black spot of roses caused by the parasitic fungus *Actinonema rosae* (Lib.) Fries. The spots, which are more or less circular in outline, are characterized by a very irregular, fibrillose border. This fibrillose character is due to the radiating strands of mycelium which occur beneath the cuticle. Appearing among the mycelial strands are numerous dark specks, the fruit bodies of the fungus. The spots may be isolated and confluent, or so numerous as to involve the entire upper surface of the leaf. Plants which are attacked become defoliated early in the season, and the leaf buds, which should remain dormant till the next year, often open late in the season. As a result, the plant is weakened so that it blossoms poorly or not at all in the following season.

Since very little is known concerning the life history of the fungus and the development of the *Actinonema* stage, an attempt has been made by cultures on artificial media and on the host to furnish a more satisfactory knowledge of this interesting organism. Before giving an account of this study it may be well to state briefly the characters of the vegetative and fruiting structures of the rose *Actinonema*.

The vegetative body of the fungus consists of two parts, the subcuticular mycelium and the internal mycelium. The subcuticular mycelium is immediately underneath the cuticle, being above the outer wall of the epidermal cells. It consists of branched, radiating strands of mycelium which anastomose, making a network. Each strand consists of several filaments united together, either side by side or sometimes superimposed. At the right of the acervulus in fig. 1 is shown a cross-section of one of these strands. The internal mycelium penetrates the mesophyll of the

[1] Contribution from the Department of Botany, Cornell University. No. 143.

leaf and furnishes nutriment for the subcuticular part. It is connected with the latter by occasional hyphae which penetrate the epidermal cells or pass between them.

A section of the fruit bodies or acervuli perpendicular to the surface of the leaf shows that they are formed between the cuticle and the outer wall of the epidermal cells. They are consequently flattened. The stroma of the acervulus is seated directly on the epidermal cells and consists of a very thin layer of small, hyaline to yellowish, pseudoparenchymatous cells. It is connected with the internal mycelium below by hyphae which extend either through or between the epidermal cells into the mesophyll. Laterally the stroma is connected with the subcuticular mycelium. There is no wall or membrane of fungous tissue covering the acervulus. On the upper side of this stroma certain cells are formed which bear the conidia. These conidiophores are not prominently differentiated in form from the other stromatic cells, but are slightly elongated upward. The conidia are hyaline, 2-celled, and oval to elliptical in outline. They are usually somewhat constricted at the septum. The conidia are formed on the somewhat pointed upper ends of the conidiophore layer. The great numbers which are produced cause such a pressure that the cuticle is finally ruptured. The cuticle, which is the only covering for the acervulus, is thus thrown back irregularly, exposing the mass of conidia and permitting their escape.

While the spots together with the mycelial strands and acervuli appear dark, this color is not due to the fungus, which is almost colorless, but to the disintegration of the cells below the spot.

Development of acervuli

It is from the subcuticular mycelium that the acervuli arise. At certain definite points the mycelium begins to form a stroma, which increases in a centrifugal manner, forming a more or less circular stromatic layer. Certain cells of this stroma which are to give rise to the conidia are directed upward as short stalks. These increase in size, forming a closely aggregated layer standing perpendicular to the stroma. Meanwhile, the mesophyll tissue directly below the acervulus is being disintegrated and a dense

tangle of fungous filaments is formed in its place. From the perpendicular cells arising from the stroma a cell is cut off by a transverse septum. This cell enlarges into an oval body, the conidium, which soon becomes septate. As the conidia are increasing in size, the pressure on the cuticle above becomes greater and greater, so that it is at length broken, leaving the margin of the exposed acervulus irregularly torn (fig. 1). Sometimes a central papilla is present which marks the place where the cuticle will rupture. At maturity the conidia are oval to elliptical and 2-celled. They are hyaline and 18–25×5–6 μ. They may be unequally septate, either straight or subfalcate, and often so deeply constricted at the line of septation that the halves fall apart readily. Several large granules and guttulae are normally present (fig. 3).

Germination of conidia

The conidia germinate within 24 hours in bean agar or in hanging drops of water. Each of the cells may first enlarge, becoming more or less spherical and vacuolate before the formation of the germ tube. Frequently only one of the cells germinates by the formation of one or two germ tubes (fig. 3). No formation of colonies was secured in poured plates of bean agar, although the fungus grows slowly when the conidia are planted on the surface, forming a small, prostrate, tawny colony. Apparently growth ceases as soon as the reserve food material within the conidium has been utilized in the development of the short hypha. This seems to occur when the hypha is 10–20 times the length of the conidium and may have become branched with several septa. If such conidia are cut out with as little of the surrounding medium as possible and transferred to bean pods, using ordinary sanitary precautions, and if the medium is spread out so as to bring the germinating conidium in contact with the pod, further growth may be induced. In two or three weeks small colonies are formed. At first the mycelium is whitish, changing to a pinkish color and becoming pale brown to blackish with age. The colonies do not spread out on bean pods, but form knots of fungous tissue often one-half as high as the diameter of the colony. The tissue of the bean which is attacked becomes blackened in a fibrillose manner,

simulating the blotch on the leaves. Conidia are formed readily on the ends of the hyphae. Such conidia are often so strongly constricted at the septum that each cell is round. There is, then, little surface of contact between the cells and they are readily separable one from the other. These spherical halves germinate in the normal manner (fig. 2). Acervuli apparently like those on the leaves are also formed on bean pods in the blackened areas. These bear conidia like the typical ones from rose leaves.

Systematic position of the conidial stage

The genus *Actinonema* is usually placed by systematists in the Sphaeroidaceae.[2] This family is a group of imperfect fungi possessing a pycnidium of the type present in *Ascochyta*, *Sphaeropsis*, etc. The pycnidium or conceptacle is more or less oval in form, with a membranaceous wall of fungous tissue, usually opening at the apex by a minute pore. Some writers speak of the fruit bodies of *Actinonema* as pycnidia[3] or perithecia.[4] FRANK[5] considered them as very flat spermagonia ("des sehr flachen Spermagoniums"). SORAUER[6] speaks of them as small astomate pycnidia ("die kleinen mündungslosen Pykniden").

It is very evident from the foregoing account that the conidial stage of the rose *Actinonema* is not of the type in which the conidia are borne in a pycnidium or perithecium. The conidia are borne in an acervulus resembling that found in the Melanconiales, as exampled by *Gloeosporium*, *Marsonia*, etc. SCRIBNER[7] has correctly figured the structure of the acervulus and says that while the fungus from analogy is placed with the sphaeriaceous fungi, no perithecia-like or pycnidial structures have been observed.

Partly because of the different interpretations of the morphology

[2] SACCARDO, P. A., Syll. Fung. **3**:408. 1884; also LINDAU, G., Sphaeropsidales in ENGLER and PRANTL'S Pflanzfam. **1**:369. 1900.

[3] LINDAU, G., *loc. cit.*

[4] MASSEE, G., Diseases of cultivated plants. 428. 1910.

[5] FRANK, A. B., Die Krankheiten der Pflanzen. 621. 1880.

[6] SORAUER, PAUL, Handbuch der Pflanzenkrankheiten. 406. 1908.

[7] SCRIBNER, F. L., The black spot on rose leaves. Rept. U.S. Dept. Agric. 366–369. *pls. 8, 9.* (1887) 1888.

of this fungus it has been variously named by different workers. In 1849 the name *Actinonema rosae* (Lib.) Fr.[8] was employed. In 1853 BONORDEN[9] described it as *Dicoccum rosae*, one of the Hyphomycetes. He says that the fungus forms small, closely aggregated pustules of a brown green color which dehisce irregularly. From collections made in 1888–1889, BRIOSI and CAVARA distributed the species under the name *Marsonia rosae* (Bon.) Br. & Cav.[10] because they recognized the acervulus type of fruit body which is characteristic of the Melanconiales. The 2-celled hyaline conidia suggested its position in the genus *Marsonia*.[11] I have been able to examine the specimens distributed by BRIOSI and CAVARA and have found them to be the same as the rose *Actinonema* in the United States. The drawing of acervulus and spores which accompany the specimens show the same structure.[12]

SACCARDO[13] notes that *Marsonia rosae* (Bon.) Br. and Cav. resembles *Actinonema rosae* (Lib.) Fr. This same fungus was described by TRAIL[14] in 1889 as occurring on roses in Scotland. He called it *Marsonia rosae*.

The characters of the genus *Actinonema* have changed from time to time since the genus was established by PERSOON.[15] He applied the name to those forms on leaves and stems having radiate sterile mycelial strands. He describes two species, *A. crataegi* and *A. caulincola*, in neither of which perithecia or conidia were observed.

In 1828, FRIES[16] included two species in the genus *Actinonema*,

[8] FRIES, ELIAS, Summa veg. Scand. 424. 1849.

[9] BONORDEN, H. F., Beiträge zur Mykologie. Bot. Zeit. 282. *pl. 7. fig. 2.* 1853.

[10] BRIOSI and CAVARA, Funghi parassiti delle coltivate od utile. n. 97. 1889.

[11] La natura degli acervuli fruitifera, subcutanei ed erompenti, ci induce a riferire questo funghetto ai Melanconiei sezione delle Didymosporee Sacc. ove trova riscontro nel genere *Marsonia* pure a spore didime e jaline.

[12] Type material was received through the courtesy of the Bureau of Plant Industry, U.S. Dept. Agric. I am greatly indebted to Miss ETHEL C. FIELD of the same Bureau for some notes on the specimens. She finds that there is no apparent difference between *Marsonia rosae* of this collection and other European material which is labeled *Actinonema rosae*.

[13] SACCARDO, P. A., Syll. Fung. **10**:477. 1892.

[14] TRAIL, J. W. H., Micromycetes of Inveraray. 46. 1889.

[15] PERSOON, C. H., Mycologia Europaea **1**:51–52. 1822.

[16] FRIES, ELIAS, Elenchus Fungorum. 151. 1828.

A. padi and *A. crataegi*, the latter showing at length perithecia-like structures, but no conidia were observed. In 1829[17] he employed the name *Actinonema* for the sterile state of fungi belonging to the Pyrenomycetes and Perisporiaceae. Later[18] he characterized the genus as having a fibrillose, radiating mycelium, a delicate perithecium, and bilocular spores, and lists *A. rosae* as one of the species which often possesses only a sterile mycelium. SACCARDO[19] employs these characters as given by FRIES and notes that the fruits have not been observed in many species. Of the 18 species of *Actinonema* which have been described, there are 8 species in which the spores were not observed at that time. The radiating fibrillose character of the mycelium has been used as the principal generic character for these species, thus employing the distinctive character as originally given by PERSOON. LINDAU[20] includes in *Actinonema* astomate pycnidial forms occurring on leaves. The pycnidia arise from radiately actinic strands of mycelium.

The genus *Marsonia* is characterized by having a *subepidermal* acervulus, in which are produced hyaline, 2-celled conidia, very similar to the conidia of *Actinonema*. Several species of *Marsonia* have been described, however, in which the acervulus is *subcutaneous*, as *Marsonia baptisiae* E. & E., *M. panatoniana* Berl., and *M. fructigena* (Rick.) Berl. BRIOSI and CAVARA recognized the true morphology of the rose *Actinonema* acervulus, but attached no significance to the fact that it was *subcuticular* and not *subepidermal*. The *Actinonema*-like character of the mycelium was not taken into account by them as indicative of generic position. TRAIL must have been of the same opinion when he named this same fungus *Marsonia rosae*.

Even though the subepidermal acervulus has been made one of the generic characters of *Marsonia*, it would seem that these subcuticular forms might properly be placed in this genus. On the other hand, we do not know the structure of the perithecia or pycnidia of other species of *Actinonema*. If we accept PERSOON'S

[17] FRIES, ELIAS, Systema Mycologicum **3**:266. 1829.

[18] ———, Summa veg. Scand. 424. 1849.

[19] SACCARDO, P. A., Syll. Fung. **3**:408. 1884.

[20] LINDAU, G., ENGLER and PRANTL'S Pflanzfam. **1**:399. 1899.

characterization of the genus, it has no fruit bodies, but consists only of sterile mycelium.

The rose fungus evidently, then, does not possess the characters of a typical *Marsonia*, nor does it agree with the original characterization of *Actinonema*. Whether these differences are worthy of good generic rank, separating it from both these genera, is a matter for consideration.

Development of the ascigerous stage

During the autumn of 1910, leaves attacked by the conidial stage were collected and placed in wire cages to winter out of doors. When some of these leaves were brought to the laboratory early in April and examined, shield-shaped structures suggestive of the perithecia of the Microthyriaceae were found to be present. At this time, however, no spores had been developed. Fig. 2 shows one of these perithecia as seen in surface view. Such preparations were made by stripping off the epidermis of the leaf together with the perithecia. By April 27 these perithecia had matured and were found to possess characters similar to the genus *Asterella*, a genus apparently including heterogeneous elements.

For the study of the development of the perithecia, material was killed in Merkel's fluid and stained with Flemming's triple stain. By killing material at different times during a period of three weeks, many of the developmental stages were obtained. Not all perithecia on the same leaf are in the same stage of development at the same time. Unfortunately the material was too far advanced for the study of fertilization and the immediate subsequent development. This in itself would be a very interesting study, since nothing is known of these phenomena in the Microthyriaceae.

The shield was found to be entirely separate in origin from the tissue which gives rise to the asci. It is formed immediately beneath the cuticle from the radiating strands of mycelium which now are thick-walled and dark brown in color. The strands themselves can be traced across the shield (fig. 4), showing that the growth begins at any point on the mycelial strand and new cells are added in a centrifugal manner. In this way a more or

less circular shield is formed, the elements of which are arranged in a radiating manner, especially noticeable at the margin of the shield. The cells which make up the shield possess thick, dark walls.

The shield varies in diameter from 100 to 250 μ, and may be more than one cell in thickness. In fig. 6 is shown a young stage in the development of a perithecium. The shield forms a thin layer above the epidermal cells or beneath the elevated cuticle. Beneath the epidermal cells, and above the palisade parenchyma, is an undifferentiated layer of fungous tissue, the stroma from which the asci later arise. This stroma is 3–6 cells in thickness and is made up of cells similar to those of the shield. Occasional filaments connect these two layers through the epidermal cells of the host. In fig. 7, when the fertile layer has increased and the fruit body has begun to be differentiated, the shield is still distinct and not connected with it at the margin. At this time the cells in the center of the young fertile stroma are thinner walled, with a more deeply staining content.

The asci are formed within the fertile stroma, arising from the basal portion, as shown in figs. 8 and 9. In this way the cells in the upper part of the fertile stroma persist, forming a delicate covering over the hymenium. The development of the asci within this fertile stroma is comparable with their origin in the apothecia of the Phacidiales. The hymenium arises in the same way, and the upper part of the stroma corresponds with the tissue which covers the hymenium before the opening of the apothecium. In the rose fungus, however, this covering is not so well developed and may not always persist to be folded back when the fruit body opens. It may form a continuous delicate layer over the asci until the fruit body is mature and only rupture together with the shield. In other cases this covering is broken by the development of the hymenial layer. Fragments may remain at the margin of the apothecium or they may disappear. It is only by the elongation of the asci and the consequent increase of pressure that the cuticle and shield, together with the upper part of the apothecium, are ruptured in an irregularly stellate manner and thrown back. The portions covering the hymenium have ruptured in fig. 11.

In the mature opened condition shown in fig. 12, the thin-walled cells of the upper part of the apothecium still persist on the margin of the fruit body. The opened perithecia present in surface view the appearance shown in fig. 5. The folding back of the shield is shown in section in fig. 15. The perithecia develop independently of the acervuli, as would be expected from the origin of the two. In fig. 13 is shown an old acervulus by the side of a perithecium. In none of the material which had wintered could acervuli be found which were bearing conidia.

The epidermal cells of the host persist for a long time, so that the ascogenous layer and shield are separated. They may become entirely destroyed as the asci elongate and the perithecium becomes mature (fig. 14), or they may persist on the margin of the mature perithecium (fig. 12). The perithecia vary in shape from spherical to discoid. One of the large discoid perithecia is represented in section in fig. 14. The septate, knobbed paraphyses extend between and beyond the asci until the time when the spores are nearly mature. Asci in many stages of development occur within each perithecium. Mature asci extend slightly beyond the paraphyses and the spores are discharged from an apical pore (fig. 16) formed by the rupture of the wall. The asci are oblong or subclavate, tapering above rather bluntly, and are 70–80×15 μ.

Apparently the spores are not discharged with violence. Agar plates were inverted above rose leaves in moist chambers, the surface of the agar coming nearly in contact with the leaf. No spores were observed to have lodged on the surface of the agar, as would be expected if they were projected forcibly from the ascus. As far as I have been able to observe, they merely pile up in a whitish heap in the opened perithecium. The spores are 20–25×5–6 μ, varying extremely in form (fig. 17), as do the conidia. They resemble the conidia very much except that they are not so strongly constricted at the septum. They are hyaline and bicellular. Usually large granules and several guttulae are present in each cell. The cells are generally unequal in size, the upper one being broader.

Germination of ascospores

Considerable difficulty was experienced in germinating the ascospores. All attempts to employ artificial media have been unsuccessful. Spores from the same preparation have been used in poured and planted plates of bean agar, in hanging drops of water, in similar drops in which has been placed a small piece of green rose leaf, in infusions made by boiling green rose leaves in water, and in drops of water on rose leaves in a moist chamber. In no case has germination been secured in any other way than by the last method. Germination occurs within 24 hours, the larger cell more often germinating, although either cell is capable of germination. A germ tube is characteristically formed at one side near the end of the spore. This hypha soon branches and septa are laid down (fig. 18). Occasionally two tubes are formed from a single cell. In about 35 transfers of spores to bean pods made under aseptic conditions no growth was secured. From these and the foregoing experiments it would seem that the ascospores are dependent on some stimulus of the living plant for germination. There may be some advantage to the parasite in this, since many spores would germinate before they are able to reach a suitable location on the host.

Artificial infection

Ascospores were used in the infection experiments. Since they are discharged in such masses in the opened perithecia, they can easily be removed free of everything else. Several series of poured plates made from spores obtained in this way remained absolutely sterile, which indicated that no other spores except ascospores of the rose fungus had been carried over. The spore masses were first removed to a drop of sterile water on a slide. With a needle, then, some of the spores were transferred to drops of water on the leaves of living roses. The plants were then covered with bell-jars and were allowed to remain covered for two days. Infections from inoculations made April 27 were very evident by May 7, appearing as small black areas. By May 15 mature acervuli and conidia of the *Actinonema* type were formed, thus completing the life cycle and connecting the two forms. Inoculations were

also made in the same way on leaves placed in Petri dishes lined with moist filter paper. In four days the radiating strands were very evident with the aid of the low power of a microscope. Infection occurs by the entrance of the germ tube through the cuticle, there being no stomata on the upper surface of the leaves. From the subcuticular mycelium, hyphae later penetrate to the tissue below, first filling the epidermal cells, and only in the advanced stages of the disease penetrating the mesophyll.

The way in which this fungus hibernates is no longer a matter of conjecture. SCRIBNER[21] suggested that the spores lodge on the buds in autumn and remain there dormant until the leaves have expanded the following summer. As has been found to be true with many imperfect fungi, this fungus is carried through the winter on fallen leaves and the ascosporic stage develops in the following spring.

This study shows that *Gnomoniella rosae* (Fkl.) Sacc. is not the perfect stage of the rose *Actinonema*, as has recently been suggested.[22] One species of *Actinonema*, however, has been connected with an *Asterella*, *Actinonema rubi* (Fkl.) becoming *Asterella rubi* (Fkl.) v. Höhnel.[23] He found in the spring the *Asterella* stage on living canes of *Rubus Idaeus*. These areas had been occupied the previous summer by the conidial stage.

The genus *Asterella* was first proposed by SACCARDO[24] as a subgenus of *Asterina* for those species which have hyaline spores. Later [25] he raised *Asterella* to generic rank. As SACCARDO himself points out, further investigation of species which are at present placed in the genus *Asterella* will result in their transfer to *Asterina*, since the spores become brown at maturity. LINDAU[26] thinks the existence of this genus is still questionable. Subsequently but little investigation has been made on the genus and no clear-cut

[21] See footnote 7.

[22] LAUBERT, R., and SCHWARTZ, MARTIN, Rosenkrankheiten und Rosenfeinde. 16–19. 1910.

[23] VON HÖHNEL, F., Über *Actinonema rubi* Fuckel ist *Asterella rubi* (Fkl.) v. Höhnel. Ann. Myc. **3**:326. 1905.

[24] SACCARDO, P. A., Syll. Fung. **9**:393. 1891.

[25] ———, Syll. Fung. **1**:25 and 42. 1882.

[26] LINDAU, G., ENGLER and PRANTL'S Pflanzfam. **1**:340. 1897.

generic limits have been proposed. One finds included species whose spores become brown, some which are aparaphysate, some possessing filiform paraphyses, and others having paraphyses which are enlarged at the tips. In fact, the whole family Microthyriaceae is but little known, due in part to the fact that most of the forms are tropical. A thorough investigation of perithecial development is necessary, since very little attention has been given to this group. The family is at present characterized by having perithecia which are shield-shaped, thin membranaceous, flat, with a rounded pore at the top and with a membrane formed *only on the upper side*. With the exception of the species on rose leaves, which I have studied, it is not known whether or not the forms without an apical pore possess one at maturity. It has long been recognized, because of the entirely different manner of development, that the Microthyriaceae are widely separated from the other two families of the Perisporiales, the Erysiphaceae and the Perisporiaceae.

In order to see if other genera of the Microthyriaceae corresponded in structure and development with the forms on rose leaves several of them were examined. *Asterina orbicularis* B. & C., n. 231 of RAVENEL'S collections, forms entirely superficial perithecia, sending hyphae partially through the cuticle. *Asterina inquinans* E. & E., n. 1785 N.A.F., is also superficial, ends of the mycelium being observed in the stomata. *Asterina plantaginis* Ellis, n. 791 N.A.F., forms spherical perithecia entirely sunken within the host tissue. The perithecia are ostiolate and appear to have the characters of a *Sphaerella*. *Micropeltis longispora* Earle, n. 6349, plants of Porto Rico, is entirely superficial. *Microthyrium littigiosum* Sacc., collected at Frankfort, Germany, by Dr. PAUL MAGNUS, seems to form superficial perithecia, but the mycelium is present in the epidermal cells. *Myriocopron smilacis* (De Not.) Sacc., n. 600 E. & E., N.A.F., also forms superficial perithecia and the mycelium occurs in the stomata. None of these representative genera seem to be comparable to the type of development as exhibited by the rose fungus. Since so little is known of the perithecial development and the method of securing food supply of the Microthyriaceae, this family would afford an

excellent field for investigation. MAIRE[27] has described the organs of absorption of *Asterina usterii* and *Asterina typhospora*. A slender filament penetrates the epidermal wall and when it has reached the cavity of the cell it enlarges and becomes profusely branched.

The opened perithecia of the rose fungus present characters indicative of a close relationship to the Phacidiales. The ragged margin of the shield suggests the ruptured outer portion of the wall of the fruit body which at first covers the hymenium. The presence of knobbed paraphyses is also a character possessed by many Discomycetes. In the Phacidiales, however, as far as can be learned, the upper or outer part of the fruit body is not separate in origin from the ascogenous stroma, nor does it possess the characteristic structure, of the shield present in the Microthyriaceae. On the other hand, it is quite probable that few of the Microthyriaceae possess a stroma within the leaf tissue as has been described for the fungus in question. The majority are apparently superficial and with a well developed wall or shield *only on the upper side*. In spite of these facts, I feel that this fungus should be placed in the Microthyriaceae. Further morphological study of other species of this genus and related genera will throw some light on the relationship of these microthyriaceous forms. Perhaps the systematic position of many of these forms will be changed as soon as the species have been satisfactorily investigated. While the possession of the shield and the hyaline 2-celled spores are characteristics which would suggest the position of the rose fungus in the genus *Asterella*, yet, as has been pointed out, this genus is not clearly limited and contains heterogeneous elements. This fungus does not seem to accord morphologically with the members of this genus in the sense in which the genus was first employed. Species representing several generic types apparently have been included in *Asterella*. Since the characters presented by this fungus are evidently those of a distinct generic type, rather than place it in the genus *Asterella*, it seems better to treat it as the type of a new genus. Because of the two separate structures, the shield

[27] MAIRE, R., Les Suçoirs des *Meliola* et des *Asterina*. Ann. Myc. **6**:124–128. *fig. 4*. 1908.

and apothecium, the name *Diplocarpon*[28] is proposed. The following description of the genus is given.

Diplocarpon, nov. gen.—Fruit bodies formed in connection with an extensive subcuticular mycelium, consisting of a subcuticular circular shield with more or less radiate elements especially at the margin, and an innate apothecium. Shield, together with the radiating strands on which it is formed, dark brown, without a central pore. Apothecium at first separate from the shield, only joined here and there by hyphae which pass between the epidermal cells. Apothecium joined with the margin of the shield at maturity. Hymenium covered by the shield and upper part of the apothecium which at maturity rupture in an irregularly stellate manner. Asci oblong to subclavate, 8-spored; paraphyses unbranched; spores elongated, 2-celled, hyaline at maturity.

A conidial stage of the *Actinonema*-type occurs in one species.

Peritheciis scutulum subcutaneum et apothecium innatum constitutis; scutulo mycelio subcutaneo, lato extenso, atro-brunneolo insidiente; margine radialiter diffuso, contextu membraneo, astomate; apothecio innato, primo scutulo separato, maturitate margine adjuncto. Peritheciis centro stellatim laciniato-dehiscentibus; ascis oblongis; paraphysibus simplicibus; sporidiis oblongo-ellipticis, bicellularibus, maturitate hyalinis.

Actinonema uni speciei cujus statum conidicum sistit.

Since this study connects for the first time the ascosporic stage with the conidial stage of the black spot of rose leaves, a brief characterization of the species is added:

Diplocarpon rosae, n.n.

Syn. *Erysiphe radiosum* Fr. Observationes Mycologicae. 207. 1824. *Asteroma rosae* Lib. Mem. Soc. Linn. **5**:404–406. 1827. *Actinonema rosae* Fr. Summa. veg. Scand. 424. 1849. *Dicoccum rosae* Bon. Bot. Zeit. 282. 1853. *Marsonia rosae* Trail. Fung. Inverar. 46. 1889. *Marsonia rosae* Br. and Cav. Funghi parassiti n. 97. 1889.

Ascigerous stage.—Perithecia epiphyllous, spherical to disciform, 100–250 μ in diameter; upper part or shield dark brown, subcuticular, formed in conjunction with the radiating strands of mycelium, circular, with a more or less radiating structure toward the margin. Lower part of fruit body disciform, subepidermal, of several layers of pseudoparenchyma cells, the outer of which are dark brown,

[28] διπλόος, "double," καρπός, "fruit."

the margin at length breaking through the epidermis and here and there becoming connected with the margin of the shield. Fruit bodies closed at first, later opening by the rupturing of the shield together with the upper part of the apothecium in an irregularly stellate manner from the center. Asci oblong or subclavate, narrowed abruptly above, 70–80×15 μ, 8-spored; paraphyses slender, enlarged abruptly at the tip, often 1-septate. Spores oblong-elliptical, hyaline, unequally 2-celled, constricted at the septum, 20–25×5–6 μ; upper cell somewhat larger, cells usually guttulate.

Conidial stage.—Spots epiphyllous, large, dark brown or blackish, with an irregular radiating border, when numerous becoming confluent and sometimes involving the entire leaf. Mycelial strands composed of several filaments, at first hyaline, forming a subcuticular network. Internal mycelium connected through the epidermis with subcuticular mycelium. Acervuli subcutaneous, covered at first by the cuticle which ruptures irregularly; conidia 2-celled, often deeply constricted, straight or subfalcate, 18–25× 5–6 μ, hyaline and guttulate.

Conidial stage appearing on rose leaves in summer and autumn often causing defoliation of the plants. Ascigerous stage appearing in the spring on fallen leaves which have remained on the ground.

Peritheciis epiphyllis, globosis v. disciformibus, 100–250 μ diam.; scutulo atro-brunneolo, subcutaneo, mycelio reticulato insidiente, orbiculare, margine plus minusve radioso. Apothecio primo epidermide tecto, demum margine scutuli adjuncto, in centro irregulari-stellato dehiscente. Ascis oblongis vel subclavatis, supra obtuse angustatis, 70–80×15 μ, octosporis; paraphysibus filiformibus, apice incrassatis, interdum 1-septatis; sporidiis oblongo-ellipticis, inaequaliter bicellularibus, ad septa constrictis, guttulatis, hyalinis, 20–25×5–6 μ.

Hab. in foliis dejectis Rosae sp.

Status conidicus: Maculis epiphyllis, atro-brunneis vel purpurascentibus, fibrillis e centro radiantibus, albido-arachnoideis; acervulis subcutaneis, sparsis, nigricantibus; conidiis constricto, 1-septatis, guttulatis, hyalinis, 18–25×5–6 μ.

Hab. in foliis vivis Rosae sp.

Susceptibility of the host

This disease occurs on nearly all the cultivated varieties of roses both out of doors and in the greenhouse. BRIOSI and CAVARA note that only four varieties, Rosa hybrida var. Belle

Angevine, Triomphe d'Alençon, Abel Grant, Rosa borboniaria var. Triomphe d'Anger, of the 600 growing in the botanical gardens at Pavia are free from the attacks of this fungus. LAUBERT and SCHWARTZ[29] call attention to the fact that the bushy sorts are more susceptible than climbing varieties, and also that thin-leaved species are most liable to attack. HALSTED[30] finds that a wild species, *Rosa humilis*, is also subject to attack when growing in a garden with diseased plants. The amount of loss caused is equaled or surpassed by only one other rose disease, the powdery mildew.

Control measures

This disease has been very satisfactorily controlled by the use of any of the standard copper compounds. Since now we know that the fungus winters over in the fallen leaves, sanitary measures may better be employed in combating the disease. If all the leaves are gathered together and burned either late in the autumn or early in the spring, before the new leaves have expanded, the chances of infection would be greatly lessened.

This investigation was undertaken at the suggestion of and under the careful direction of Professor GEORGE F. ATKINSON, Cornell University, to whom I am very grateful for help and criticism.

AGRICULTURAL EXPERIMENT STATION
AUBURN, ALABAMA

NOTE.—Since this manuscript has been sent to the publishers, I have received type specimens of *Asterella rubi*, which had been sent to Professor GEORGE F. ATKINSON, through the courtesy of Professor F. VON HÖHNEL. Because of the fact that *Asterella rubi* is the first *Asterella* to be connected with an *Actinonema*, and is one of the most recently described species of this genus, it is especially important that it be compared morphologically, with the rose fungus.

For the study of the structure of the fruit bodies of *Asterella rubi* the cortex of some of the affected raspberry canes was imbedded in paraffin and sectioned. The perithecia were found to possess a central pore or ostiolum. They are *entirely* superficial and with a well developed structure only on the upper side. There is no well defined stroma from which the asci arise.

By treating small pieces of the cortex with lactic acid the entire shield may

[29] See footnote 22.

[30] HALSTED, B. D., New Jersey Agr. Exp. Sta. Rept. **13**:281. (1892) 1893.

be loosened, and can be floated away, thus proving beyond a doubt that this structure is wholly superficial and not subcuticular. *Asterella rubi*, therefore, conforms to the present concept of the genus *Asterella*, but is of an entirely different generic type from that represented by *Diplocarpon rosae*.

EXPLANATION OF PLATE XIII

FIG. 1.—Acervulus of conidial stage (*Actinonema rosae*), with a section of one of the radiating strands at the right of the acervulus; ×400.

FIG. 2.—Conidia formed free in culture; the two halves are easily separable; germination of the separated cells; ×400.

FIG. 3.—Normal conidia from acervuli, and their method of germination; ×400.

FIG. 4.—Surface view of *Diplocarpon rosae*, showing the shield and subcuticular strands from which it developed; ×110.

FIG. 5.—Surface view of mature perithecia in which the shield has been ruptured irregularly and folded back; ×55.

FIG. 6.—A very young stage in the development of a fruit body in which the shield and the stroma from which the asci are formed are distinct; *C*, cuticle; *B*, epidermal cells; *D*, ascogenous stroma; ×200.

FIG. 7.—A stage in which the fruiting part of the perithecium has begun to be differentiated; the shield and ascogenous stroma are separate; *A*, young apothecium; ×200.

FIG. 8.—Differentiation of the asci within the apothecium; ×200.

FIG. 9.—Perithecium in which the epidermal cells still persist between the apothecium and shield; the thin-walled cells of the upper part of the apothecium form a covering over the hymenium; ×200.

FIG. 10.—Perithecium in about the same stage of development as fig. 9, but the shield and fertile stroma are completely united; ×200.

FIG. 11.—Perithecium which is nearly mature; the hymenial covering has broken; *A*, upper part of apothecium; *B*, shield; *C*, cuticle; *E*, epidermal cells; ×200.

FIG. 12.—Mature fruit body of *Diplocarpon rosae;* some of the cells of the upper part of the apothecium persist at the margin; ×200.

FIG. 13.—An old acervulus persisting at the side of a perithecium; ×200.

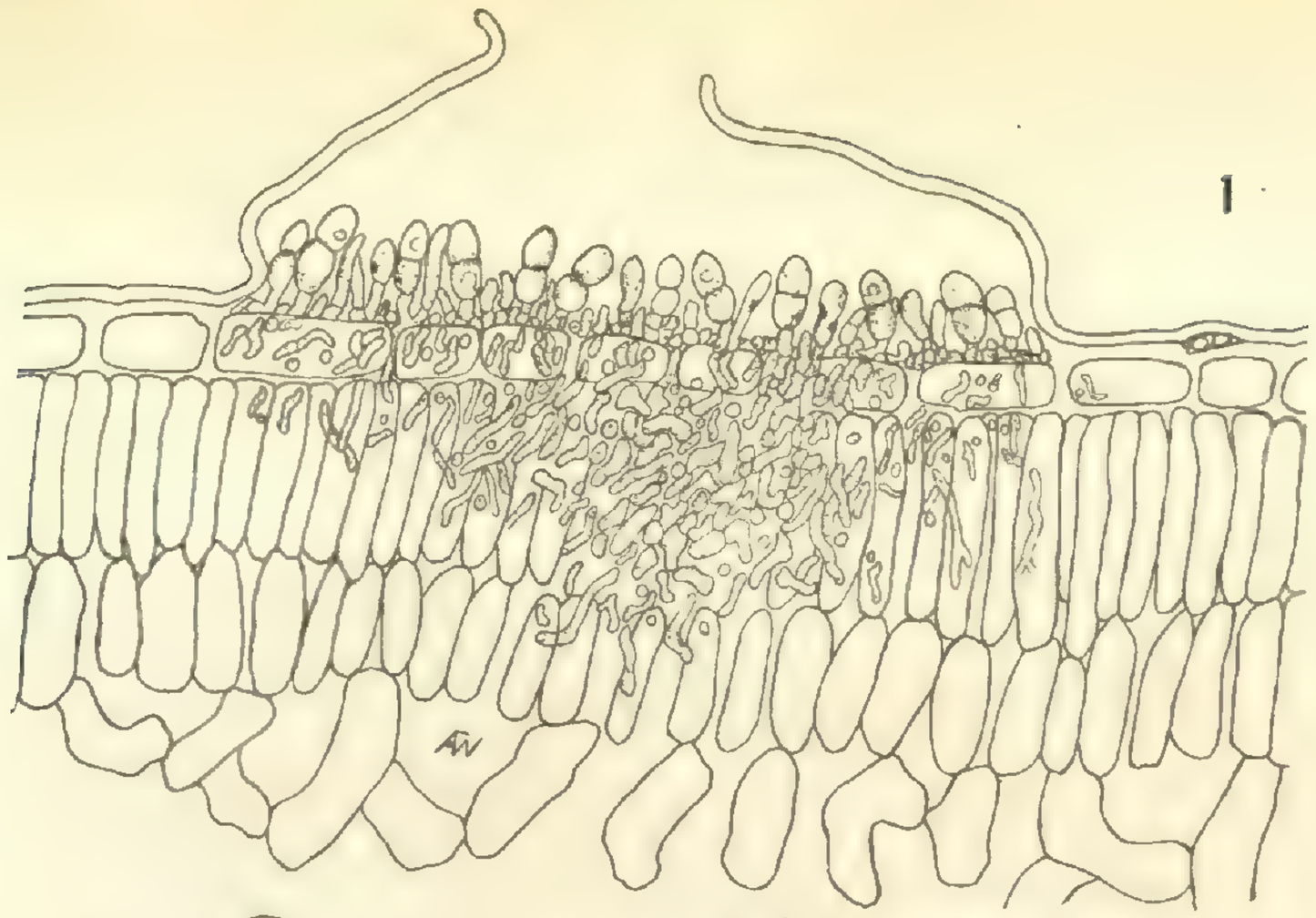
FIG. 14.—A large disciform perithecium; some asci are mature and in others the spores have not yet been formed; the ascogenous stroma and shield have grown together and the epidermal cells have been destroyed; ×200.

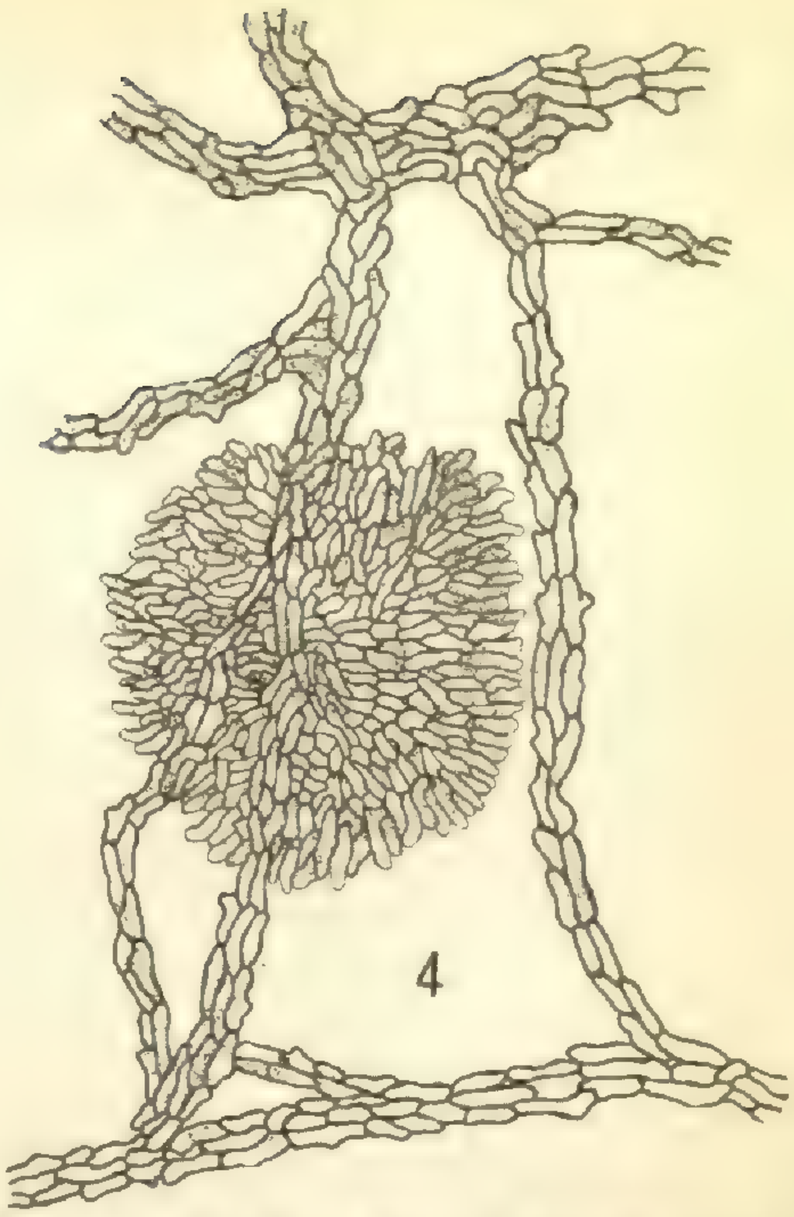
FIG. 15.—Section through a mature perithecium, showing the manner in which the shield is folded back; ×200.

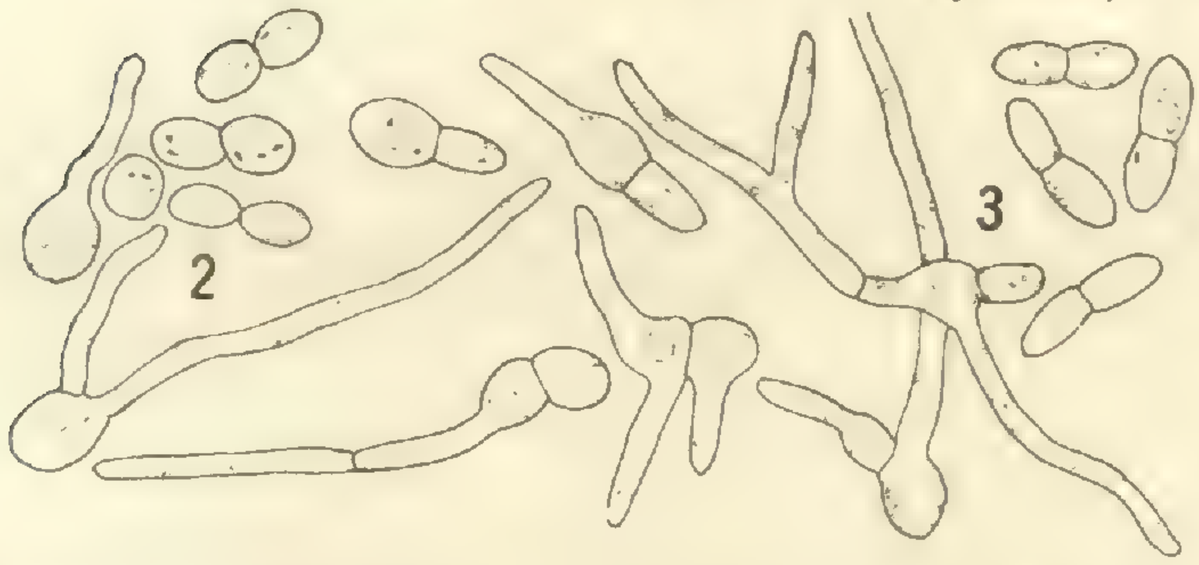
FIG. 16.—Mature asci and paraphyses; the spores have been discharged apically from one ascus; ×400.

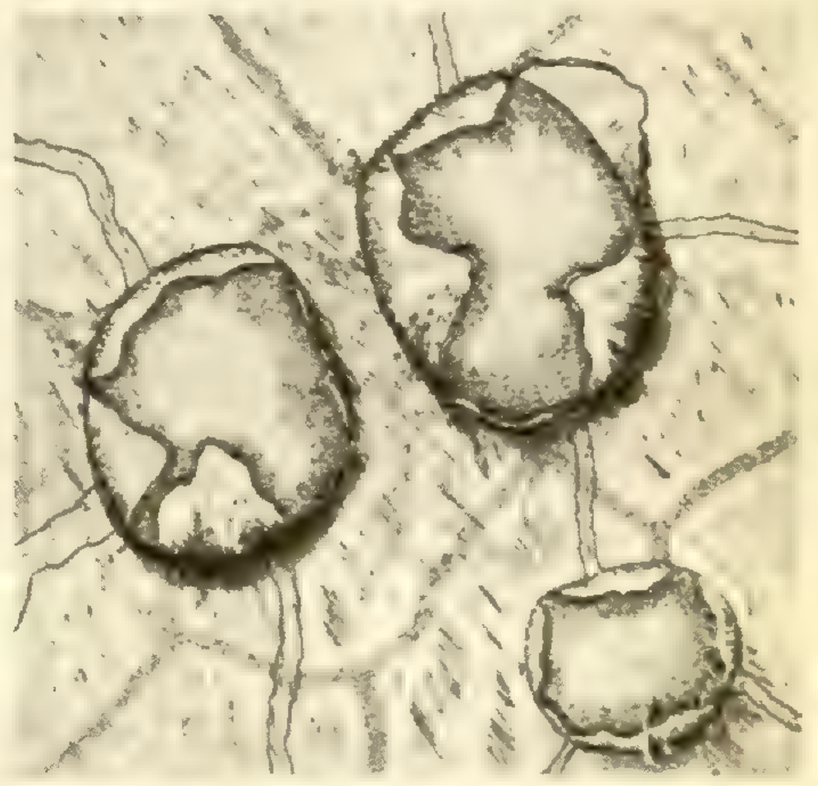
FIG. 17.—Ascospores of *Diplocarpon rosae;* ×400.

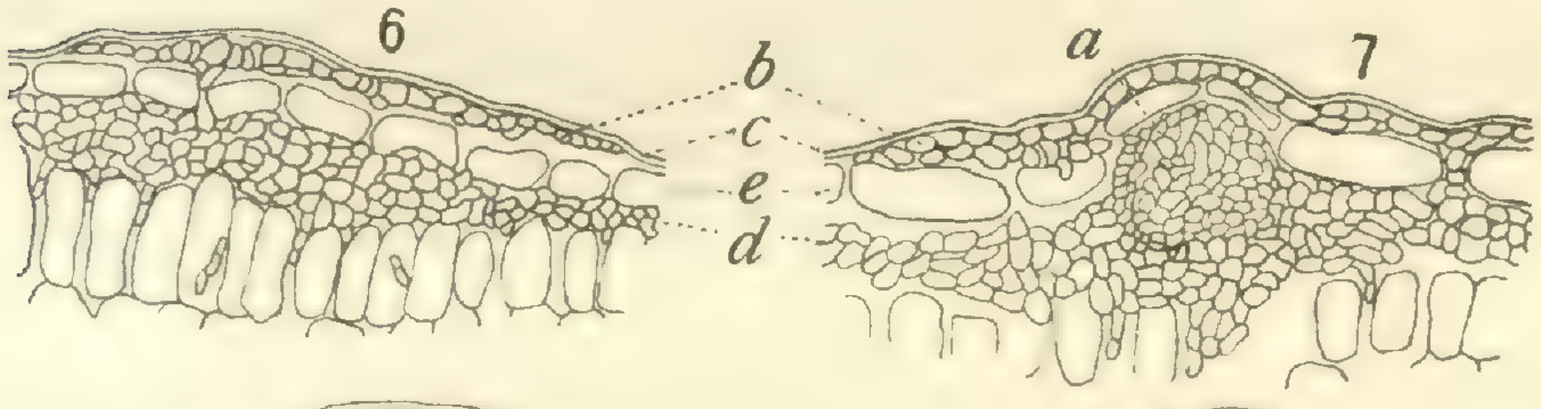
FIG. 18.—Germination of ascospores; ×400.

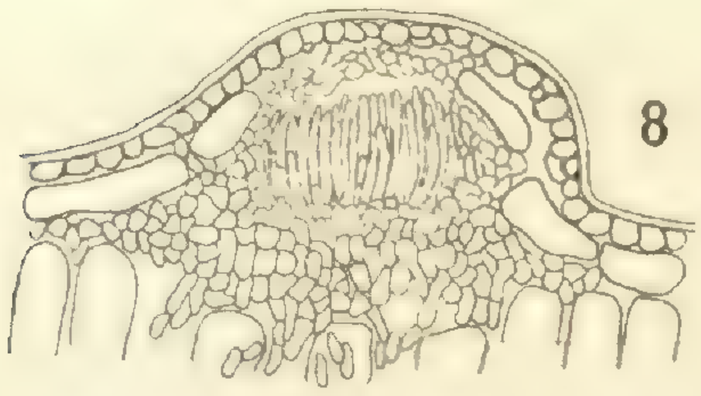


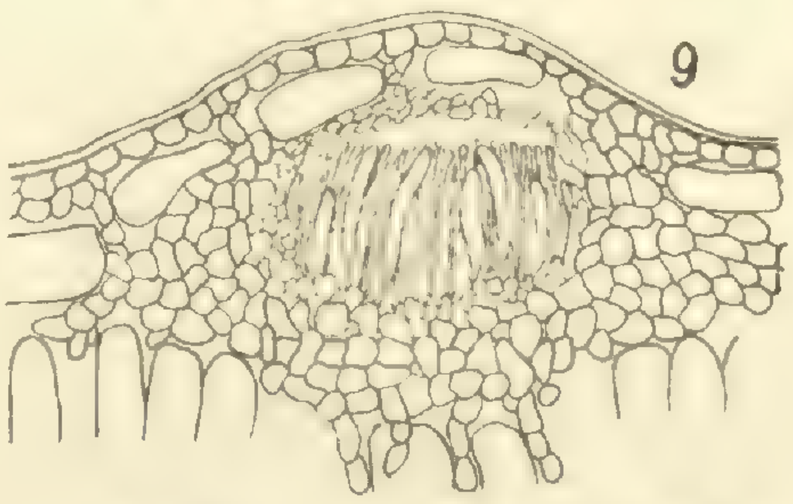


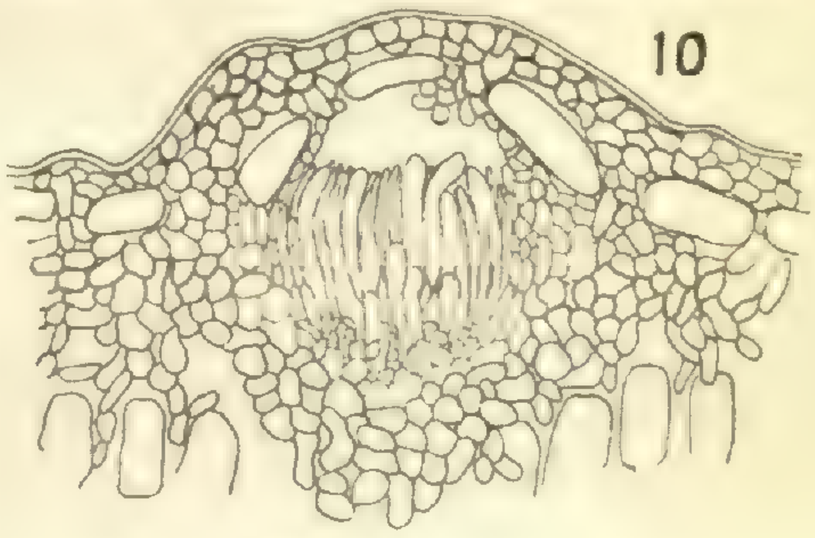


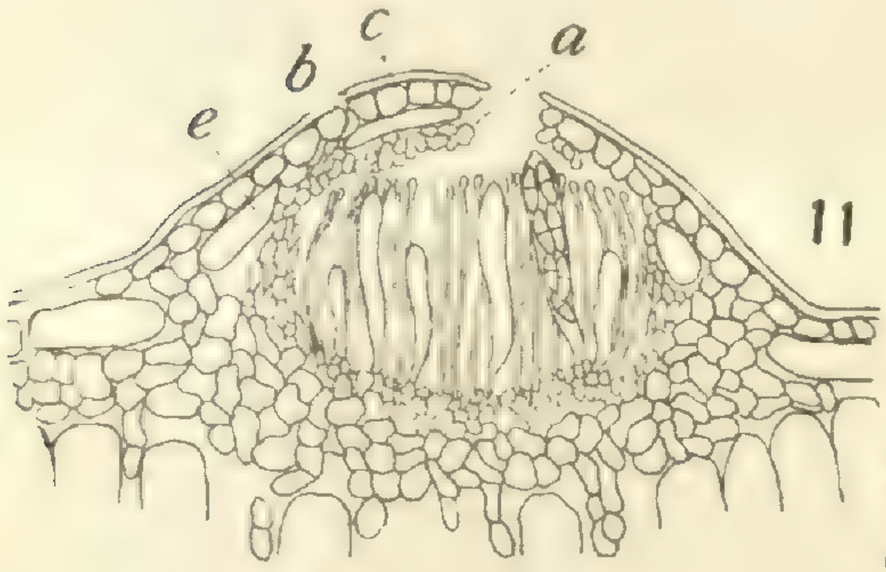


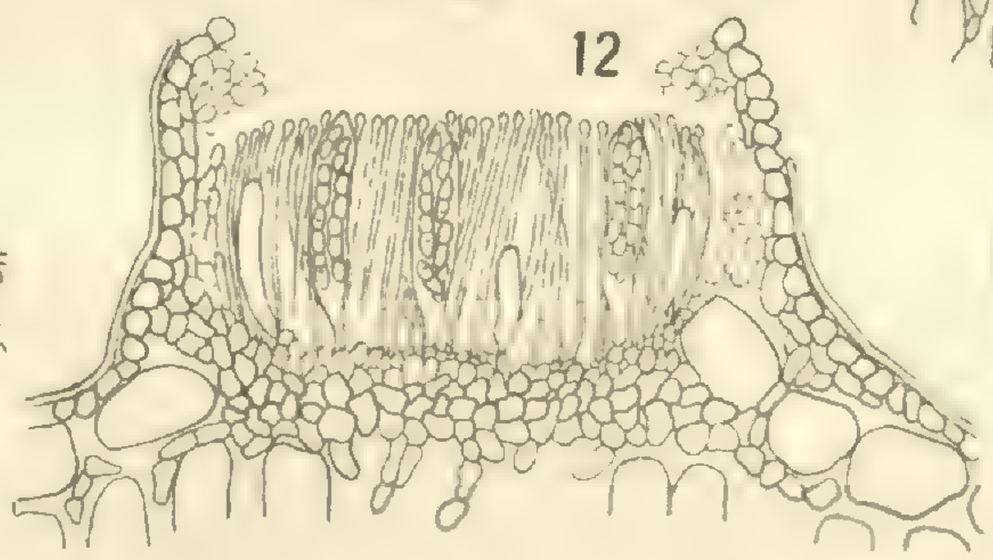


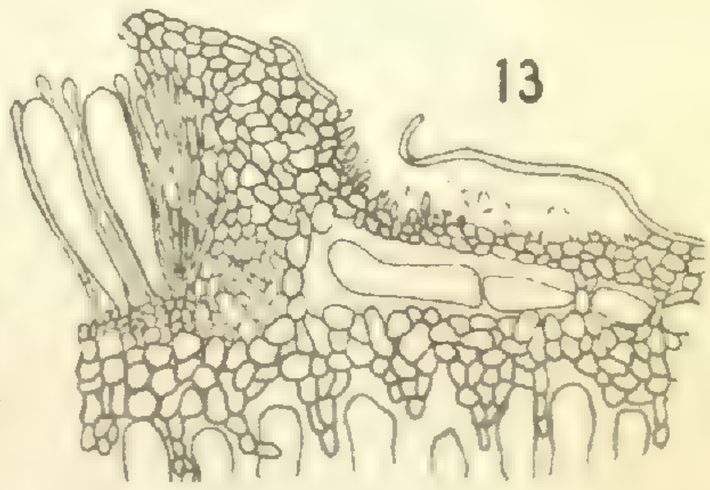


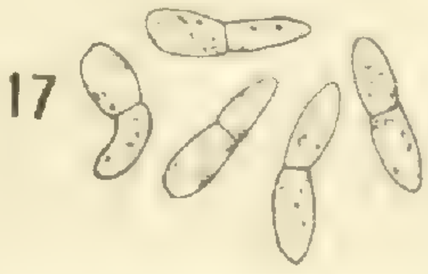


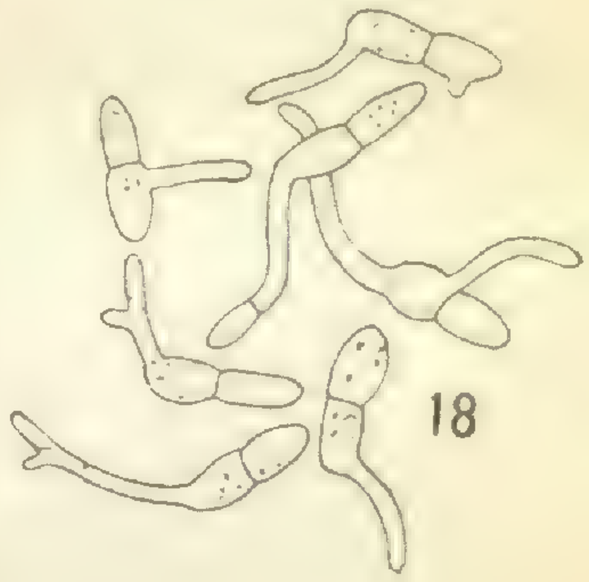












WOLF on ACTINONEMA ROSAE

F138-214

UNDESCRIBED PLANTS FROM GUATEMALA AND OTHER CENTRAL AMERICAN REPUBLICS. XXXV[1]

JOHN DONNELL SMITH

Rigiostachys quassiaefolia Donn. Sm.—Folia maxima 3–5-foliolata, rhachi petioloque alatis. Racemi axillares petiolo pluries breviores. Sepala minuta deltoidea. Discus vix ullus. Ovaria obovoidea, stylis lateralibus, ovulis geminis.

Omnino glabra. Foliola plerumque 5 sessilia integra lanceolato-elliptica utrinque acuminata, terminali ceteris paulo majore 12–14 cm. longo 4.5–5 cm. lato, rhachi oblanceolata 3.5–4 cm. longa 8–10 mm. lata, petiolo 3.5–5.5 longo anguste alato. Racemi e basi floriferi circiter 10-flori rhachis 4–5 mm. longa crassa paleaceo-bracteosa, pedicelli 1.5–2.5 mm. longi. Sepala aegre 1 mm. longa. Petala oblongo-elliptica 3.5 mm. longa. Gynophorum leviter compressum 1 mm. altum atque latum. Ovaria leviter compressa 2 mm. longa mox libera, stylis praeter stigmata diu connexa discretis, ovulis paulo supra basin loculi affixis. Cetera desunt.—Specimina incompleta speciem quamvis abnormem tamen satis certam *Rigiostachydis* sistere videntur.

Panzal, Depart. Baja Verapaz, Guatemala, alt. 1000 m., Apr. 1907, *H. von Tuerckheim* n. II. 1714.

F222-3060

Eugenia (Sect. AUTEUGENIA Niedenzu; § *Biflorae* Berg.) **fiscalensis** Donn. Sm.—Glabra. Folia coriacea ex orbiculari-ovato ovata gradatim obtuseque acuminata basi rotundata. Pedunculi axillares singuli vel bini, pseudo-terminales 6–8-ni, petiolo bis terve floribus paulo longiores basi et sub flore bibracteolati. Petala oblongo-elliptica.

Arbusculus 6-metralis, ramulis dichotomis, novellis compressis purpurascentibus punctulatis, internodiis folio brevioribus. Folia nitida concoloria supra pellucido-subtus-fusco-punctulata 30–37 mm. longa 17–25 mm. lata, margine cartilagineo revoluto, nervis praeter medium supra impressum subtus prominentem parum manifestis, petiolo canaliculato 2–3 mm. longo. Pedunculi 5–7 mm. longi basi et sub flore articulati punctulati, bracteolis eciliolatis, basalibus lineari-lanceolatis 1.5 mm. longis, apicularibus subulatis vix 1 mm. longis, floribus praeter discum pubescentem glabris. Calycis tubus hemisphaericus 1.5 mm. altus, lobi semiorbiculares concavi trinervii inaequales 1–2 mm. longi in alabastro erubescentes. Petala punctulata 4.5 mm. longa

[1] Continued from BOT. GAZ. **52**:53. 1911.

genitalibus subaequilonga. Discus 2 mm.-diametralis. Bacca ignota.—*E. surinamensi* Miq. proxima.

In praeruptis *Barranca* dictis prope Fiscal, Depart. Guatemala, Guatemala, alt. 1100 m., Jun. 1909, *Charles C. Deam* n. 6226.—Typus in herb. Musei Nationalis numero proprio 579586 signatus servatur.

Anguria pachyphylla Donn. Sm.—Folia trifoliolata, foliolis breviter petiolulatis coriaceis acuminatis integris, terminali obovato basi cuneato, lateralibus oblongo-ovatis asymmetricis. Flores masculini sessiles. Calycis dentes minuti. Antherae lineares, appendice ovali glabra, loculis rectis.

Robustissima glaberrima resinulas exsudans. Caulis cum petiolo communi 3–3.5 cm. longo crassus angulato-sulcatus compressus. Foliola subaequalia 16–22 cm. longa 8.5–11 cm. lata acute incurvo-acuminata margine integerrima nervis validis subtus elevatis utrinque 7–8 penninervia aetate provectiore glandulis resinosis adspersa in sicco supra glaucescentia subtus pallidiora, foliola exteriora inaequilateralia basi intus acuta extus late rotundata, petiolulis complanatis 8–12 mm. longis. Cirrhi crassimi longissimi teretes striati. Pedunculi tantum masculini suppetentes 25–40 cm. longi complanati striati, spica 9–13 mm. longa resinosa, floribus 20–26 ex schedula Tonduziana latericiis. Calyx ellipsoideo-oblongus 9 mm. longus 3 mm. latus striatus faucibus haud constrictus basi obtusus, dentibus crassis triangularibus 1 mm. longis glandula saepius apiculatis. Petala erecta carnosa subtus elevato-costata ceterum enervia utrinque dense papillosa ungue 0.5 mm. longo exempto orbicularia 3 mm.-diametralia. Antherae 8 mm. longae 1 mm. latae, appendice 1 mm. longa. Flores feminini et fructus desiderantur.—*A. pallidae* Cogn. proxima.

In apricis ad praedium *Tuís* dictum, Prov. Cartago, Costa Rica, alt. 650 m., Nov. 1897, *Adolfo Tonduz* n. 11535.—In fruticetis apud Las Vueltas, Tucurrique, Prov. Cartago, Costa Rica, alt. 635 m., Apr. 1899, *Adolfo Tonduz* n. 13007.

CUCURBITACEARUM duas species ineditas peregrinas fas mihi sit hoc loco describere, nempe:

Anguria tabascensis Donn. Sm.—Folia dimorpha profunde bipartita vel trifoliolata. Flores masculini spicati. Calycis tubus triente superiore angustatus, dentes elongato-triangulares. Antherae breves oblongae submuticae, loculis rectis.

Glabra. Caulis tenuis striatus sulcatus. Petioli 17–27 mm. longi. Foliorum segmenta vel foliola cuspidata margine sinuosa penninervia, bipartitorum segmentum alterum oblongum 15 cm. longum 8 cm. latum intrinsecus excisum extrinsecus basi 3.5 cm. lata truncatum altero lanceolato-oblongo bis majus, trifoliatorum foliolum terminale obovatum 10 cm. longum 5 cm. latum deorsum attenuatum, lateralia oblonga 9 cm. longa 4 cm. lata intrinsecus excisa

extrinsecus basi rotundata, petiolulis 6–7 mm. longis. Cirrhi compressi striati. Pedunculi solum masculini visi striati sulcati 17–25 cm. longi, spica 4–5 cm. longa. Calycis tubus striatus subcylindricus 10 mm. longus basi obtusus, dentes 2 mm. longi erecto-patuli. Petala erecto-patula utrinque leviter furfuracea ungue 1 mm. longo atque lato exempto orbicularia 6 mm.-diametralia. Antherae 4 mm. longae 1.5 mm. latae, appendice minutissima papillosa. Flores feminini et fructus ignoti.—Ad *A. diversifoliam* Cogn. floribus arcte accedens ab ea foliis longe distat.

Ad ripas paludosas fluminis *Macayal* dicti, Comarca de Tabasco finibus Guatemalensibus adjacens, Mexico, Jul. 1889, *José N. Rovirosa* n. 519.

Gurania brachyodonta Donn. Sm.—Folia pedatim 5-foliolata, foliolis integris vel vix lobatis, interioribus obovatis deorsum attenuatis, extimis semiovatis. Flores masculini racemosi. Calycis dentes subulati tubo 2–4-plo petalis paulo breviores. Antherae lanceolato-oblongae, appendice papillosa, loculis replicatis.

Caulis tenuis cum petiolo communi complanato 5.5–9 cm. longo striatus sulcatus parce patenterque pilosus. Foliola tenuiter membranacea acute acuminata minute remoteque spinuloso-denticulata supra bulboso-pilosiuscula subtus nervis pubescentia, terminale 10.5–16.5 cm. longum 4–6 cm. latum integrum vel latere altero ad medium repando-vel angulato-sublobatum, intermedia paulo minora integra, extima 7–9 cm. longa 3.5–4.5 cm. lata intrinsecus excisa extrinsecus basi late rotundata integra vel ad instar terminalis sublobata, petiolulis propriis atque communibus complanatis striatis glabrescentibus. Cirrhi tenues striati glabrescentes. Pedunculi tantum masculini visi 9.5–14 cm. longi tenues striati glabri, racemo 7 mm. longo, pedicellis 3–22 puberulis 4–7 mm. longis, floribus ex scheda cl. repertoris luteis. Calycis ferme glabri tubus ovoideo-oblongus 6–9 mm. longus 3–4 mm. latus apice vix constrictus basi cuneatus, dentes 2–2.5 mm. longi erecto-patentes. Petala erecto-patentia oblonga 3 mm. longa 1 mm. lata acuta trinervia extus leviter papillosa. Antherae 3–4 mm. longae 1 mm. latae, appendice 0.5 mm. longa, connectivo angusto. Flores feminini et fructus ignoti.—*G. pedatae* Sprague proxime affinis differt calycis dentibus in genere brevissimis.

Ad praedium *El Recreo* dictum, Prov. Manabi, Ecuador, *Eggers* n. 15084.—In silvis prope Balao, Ecuador, Maj. 1892, *Eggers* n. 14691.

GARYA LAURIFOLIA Benth., var. **quichensis** Donn. Sm.—Folia nitida integerrima. Inflorescentia masculina densissimiflora, spicis corymboso-paniculatis suberectis abbreviatis, nodis et spiciferis et floriferis approximatis.

Frutex 2–3-metralis totus siccitate nigricans. Paniculae ex solis exemplis masculinis notae 4–6 cm. longae, internodiis 1 cm. non excedentibus.

Versus cacumen montis haud procul a San Miguel Uspantán siti, Depart. Quiché, Guatemala, alt. 1800 m., Apr. 1892, *Heyde* et *Lux*, n. 3175 ex Pl. Guat. etc. quas ed. Donn. Sm.

Alloplectus ruacophilus Donn. Sm.—Folia oblongo-elliptica vel-lanceolata utrinque acuminata mucrone denticulata. Pedunculi numerose aggregati inaequilongi. Calyx leviter obliquus, segmentis parum inaequalibus inciso-dentatis. Corolla calyce bis longior cylindracea postice saccata ore obliqua, lobis subaequalibus brevibus obtusis. Antherae rotundato-quadratae.

Caulis obtuse tetragonus glabrescens epidermatis squamellis retroversis interdum munitus ad apicem versus pilosus flavicans. Folia leviter disparia papyracea pellucida discoloria supra sparsim paleaceo-strigillosa subtus nervis fuscis pilosa ceterum strigillis minutis conspersa 15–20 cm. longa 5–6 cm. lata, nervis lateralibus utrinque 6–7 marginem ultra medium attingentibus, petiolis pilosis 2.5–5.5 cm. longis ad articulationem glandula sanguinea utrinque munitis. Pedunculi 6–12-ni 1–3 cm. longi pilosi bracteis sanguineis integris extus pilosis lanceolato-ovatis 1–1.5 cm. longis fulti. Calycis sanguinei segmenta basi extus pilosa ceterum subglabra, quatuor lanceolato-ovatis 1.5 cm. longis 7 mm. latis, quinto aequilongo dimidio angustiore, dentibus lateralibus utrinque 7 sicut apex nigro-mucronulatis. Corolla erubescens villosa 28–30 mm. longa 7 mm. lata recta vix ventricosa faucibus haud contracta, lobis 1.5 mm. longis. Stamina ad 4 mm. supra basin corollae inserta 16 mm. longa, antheris 2 mm. longis atque latis. Disci glandula solitaria. Ovarium ovoideum villosum. Fructus ignotus.—Ad *A. tetragonum* Hanst. et *A. Ichthyodermatem* Hanst. arcte accedens differt praesertim corolla.

In silvis montis vulcanici *Barba* dicti, Prov. Heredia, Costa Rica, alt. 2500–2700 m., Febr. 1890, *Adolfo Tonduz* n. 1997.—Volcán Poás, Prov. Alajuela, Costa Rica, alt. 2400 m., Mart. 1896, *John Donnell Smith*, n. 6729 ex Pl. Guat. etc. quas ed. Donn. Sm. (Specimina sub *A. Ichthyodermate* Hanst. olim distributa.)—In silvis ad Achiote in monte vulcanico *Poás* dicto, Prov. Alajuela, Costa Rica, alt. 2200 m., Dec. 1896, *Adolfo Tonduz* n. 10799.

Alloplectus tucurriquensis Donn. Sm.—Folia obovato-elliptica sensim acuminata deorsum attenuata in petiolum decurrentia inaequilateralia crenulato-denticulata. Pedicelli in racemo brevissimo dense aggregati bractea sanguinea fulti. Calyx leviter obliquus pedicello subdimidio longior plus minus sanguineus, segmentis subaequalibus oblongis integris. Antherae oblongae.

Caulis epiphytalis glaber. Folia 18–28 cm. longa 9–14 cm. lata pergamentacea supra strigilloso-pubescentia subtus puberula grosse reticulata, nervis lateralibus utrinque 9–10, petiolis 2–4 cm. longis tenuibus alatis. Racemorum

in exemplo unico suppetente haud satis evolutorum pedunculus 5–7 mm. longus, pedicelli subfasciculati 13–18 mm. longi, bracteae optime ellipticae 26–33 mm. longae 13–17 mm. latae integrae reticulato-venosae deciduae. Calyx 20–28 mm. longae ad tres partes partitus extus puberulus intus glaber irregulariter sanguineo-maculatus, segmentis obtusis reticulato-venosis. Corolla tantum immatura cognita pubescens. Antherae 5 mm. longae. Disci glandula solitaria. Ovarium cinereo-pubescens oblongo-ovoideum 8 mm. longum. Fructus ignotus.—*A. macrantho* Donn. Sm. quam maxime affinis.

In silvis prope Las Vueltas, Tucurrique Prov. Cartago, Costa Rica, alt. 635–700 m., Mart. 1899, *Adolfo Tonduz* n. 13042.

Alloplectus oinochrophyllus Donn. Sm.—Folia leviter disparia obovato-elliptica sursum cuspidato-deorsum cuneato-acuminata integra subtus vinicoloria. Calyx virescens basi saccatus, segmentis parum inaequalibus lanceolato-ovatis integris. Corolla recta triente lobata. Antherae oblongae.

Epiphytalis, caule subtetragono rufescente articulato-piloso, internodiis, 4–7 cm. longis. Folia ferme glabra 8–12 cm. longa 3–5 cm. lata, altero in pare subtriente minore, plerumque inaequilateralia falcata, nervis lateralibus utrinque 4–5 subtus fuscentibus, petiolo piloso 1–2 cm. longo. Pedunculus in utraque axilla solitarius teres pilosus 7–9 mm. longus bracteis sanguineis lanceolatis 13 mm. longis fultus, floribus minute parceque strigillosis. Calycis segmenta basi connata 30–32 mm. longa 13–17 mm. lata longe attenuata, postico ceteris simili eis paulo minore. Corollae albae (cl. repertor in schedula), venuloso-reticulatae tubus supra basin saccatam leviter ventricosus dein sensim paulo ampliatus faucibus haud constrictus 3 cm. longus, limbus obliquus, lobi suborbiculares 1 cm. longi crenulati. Stamina ad 7 mm. supra basin corollae inserta, filamentis 15 mm. longis, antheris 5.5 mm. longis basi discretis. Disci glandula solitaria acute ovata 2 mm. longa. Ovarium ovoideum cum stylo 8–10 mm. longo pubescens, stigmate bilobo. Fructus desideratur.—*A. strigoso* Hanst. affinis.

In silvis ad Pansamalá, Depart. Alta Verapaz, Guatemala, alt. 1250 m., Maj. 1887, *H. von Tuerckheim*, n. 1080 ex Pl. Guat. etc. quas ed. Donn. Sm. (Sub *A. strigoso* Hanst. olim distributus.)—In silvis montanis prope Cobán, Depart. Alta Verapaz, Guatemala, alt. 1350 m., Aug. 1907, *H. von Tuerckheim* n. II. 1918.

Quum *Alloplecti* quaedam species in America Centrali nuperius repertae sub sectionibus auctorum non satis bene militent, clavis specierum Centrali-Americanarum adhibeatur nova opportet.

I. Calyx regularis.
  A. Antherae oblongae. *A. multiflorus* Hanst.
  B. Antherae rotundato-quadratae. *A. calochlamys* Donn. Sm.

II. Calyx leviter obliquus.
A. Antherae latiores quam longiores. *A. tetragonus* Hanst.
B. Antherae rotundato-quadratae.
1. Caulis squamelliferus.
a. Corolla calycem paulo superans. *A. Ichthyoderma* Hanst.
b. Corolla calycem bis superans. *A. ruacophilus* Donn. Sm.
2. Caulis nudus.
a. Calycis segmenta inciso-crenata. *A. Forseithii* Hanst.
b. Calycis segmenta filiformi-laciniata.
† Folia in pare aequalia. *A. costaricensis* Dalla Torre et Harms.
†† Folia in pare dimorpha. *A. metamorphophyllus* Donn. Sm.
C. Antherae oblongae.
1. Folia peltata. *A. pellatus* Oliver
2. Folia basi petiolata.
a. Flores singuli aut fasciculati. *A. macrophyllus* Hemsl.
b. Flores racemosi.
† Bracteae virescentes. *A. macranthus* Donn. Sm.
†† Bracteae sanguineae. *A. tucurriquensis* Donn. Sm.

III. Calyx basi saccatus.
A. Calycis segmenta parum inaequalia.
1. Folia concoloria. *A. strigosus* Hanst.
2. Folia subtus vinicoloria. *A. oinochrophyllus* Donn. Sm.
B. Calycis segmentum posticum ceteris multo minus.
1. Pedunculus multiflorus. *A. ventricosus* Donn. Sm.
2. Pedunculi uniflori.
a. Pedunculi bini. *A. stenophyllus* Donn. Sm.
b. Pedunculi 4–5-ni. *A. coriaceus* Hanst.

F262.636 **Besleria** (§ GASTERANTHUS Benth.) **acropoda** Donn. Sm.—Folia lanceolato-elliptica utrinque acuminata serrata. Pedunculi pseudo-terminales bini triflori. Calyx amplus, segmentis integris. Corolla prona infundibuliformis calyce subtriplo longior in saccum inflatum segmento calycino pendulo paulo breviorem producta.

Frutex terrestris, ramis junioribus subtetragonis sulcatis strigilloso-pubescentibus. Folia membranacea supra glabra subtus nervis venulisque pubescentia ceterum albo-maculata supra medium grosse remoteque serrata 10–13 cm. longa 4.5–5.5 cm. lata in eodem jugo parum aequalia, nervis lateralibus utrinque 8–9, petiolis 1–2 cm. longis strigilloso-pubescentibus. Pedunculi tantum ad rami apicem siti ramulo nascente comitati demum axillares ita solitarii evadentes 15–25 mm. longi glabri, pedicellis 7–10 mm. longis glabris, floribus pube moniliformi adspersis. Calycis herbacei valde obliqui segmenta fere sejuncta, antica lanceolata 12 mm. longa, lateralia lanceolato-ovata 14 mm.

longa valde inaequilateralia semicordata, posticum orbiculari-ovatum 10 mm. longum graciliter cuspidatum. Corollae luteae tubus 3 cm. longus leviter ventricosus parum incurvatus limbi amplitudine subtriplo longior, saccus pendulus ellipsoideus 8–9 mm. longus segmento calycino postico semiamplectus, os obliquum, lobi breves arcuati. Stamina paulo supra basin tubi inserta 9 mm. longa, antheris suborbicularibus. Discus postice incrassatus. Ovarium glabrum valde obliquum ovatum 3 mm. longum, stylo 8 mm. longo. Fructus ignotus.

In silvis ad Tsaki, Talamanca, Comarca de Limón, Costa Rica, alt. 200 m., Apr. 1895, *Adolfo Tonduz* n. 9554.

F147-918

Phyllanthus (§ EUPHYLLANTHUS Griseb.) **leptobotryosus** Donn. Sm.—Folia inter maxima coriacea nitida oblongo-elliptica utrinque acuta, petiolo apice incrassato geniculato. Flores dioici. Thyrsi masculini pluri-aggregati capillacei flaccidi pubescentes, calycis segmentis disci glandulas liberas bis superantibus, filamentis totis fere connatis.

Arborescens ut videtur, ramulis glabris, novellis angulosis. Folia 12–20 cm. longa medio 5–8 cm. lata concoloria minute reticulata areolis pellucida, nervis lateralibus fortioribus utrinque 6–7, petiolis 18–23 mm. longis canaliculatis, stipulis nullis. Thyrsi tantum masculini visi 3–11 e pulvinulo oblongo-elliptico pubescente progredientes pedunculo 2–4 cm. longo computato 4–10 cm. longi laxe ramosi parce flori minute bracteolati, pedunculo rhachi axibus trichoideis, cymulis trifloris, flore medio subsessili, pedicellis lateralibus 1 mm. longis. Calycis 6-partiti segmenta parce pubescentia rhomboideo-ovalia 1 mm. longa medio incrassata margine membranacea. Disci glandulae obovatae filamenta subaequantes. Antherarum rimae horizontales.

Santo Domingo de Golfo Dulce, Comarca de Puntarenas, Costa Rica, Mart. 1896, *Adolfo Tonduz*, n. 7332 ex Pl. Guat. etc. quas ed. Donn. Sm. (n. 9937 herb. nat. Cost.).

F147-503

Hieronyma guatemalensis Donn. Sm.—Folia supra sparsim subtus densissime lepidota obsolete pilosa oblongo-obovata vel-elliptica acuminata deorsum attenuata petiolo multoties longiora. Pedicelli masculini bracteolam aequantes calyce dimidio breviores, floribus pentameris.

Ramuli petioli racemi calyces ad instar paginae inferioris foliorum lepidoti ceterum glabri. Folia 8–11 cm. longa 3.5–4.5 cm. lata incurvo- vel cuspidato-acuminata supra lepidibus albis punctata subtus lepidibus contiguis vel imbricatis rubiginosis obtecta, petiolo canaliculato 2–2.5 cm. longo, stipulis deciduis. Racemi tantum masculini visi ad apicem ramuli versus conferti paniculato-ramosi 5–8 cm. longi, bracteis deciduis, bracteolis late ovatis 1 mm. longis acutis. Calyx depresso-campanulatus 1.5 mm. altus, dentibus 5 triangularibus

minutis. Discus cupulatus 5-partitus extus glaber intus glandulosus pubescens. Stamina 5, filamentis glabris 1.8 mm. longis, loculis ovoideis 0.3 mm. longis. Ovarium rudimentarium exiguum. Flores feminini et fructus desunt.—Ex affinitate *H. oblongae* Muell. Arg.

In silvis prope Cobán, Depart. Alta Verapaz, Guatemala, alt. 1400 m., Apr. 1879, *H. von Tuerckheim*, n. 423 ex *Flora Guat. a Keck edit.*—In summo jugo inter Tactic et Cobán, Depart. Alta Verapaz, Guatemala, alt. 1850 m., Apr. 1908, *H. von Tuerckheim* n. II. 2228.

Ab hac specie specimina a *Herbert H. Smith* in Colombia lecta numero 1952 signata sub nomine erroneo ut videtur, nempe *H. laxiflora* Muell. Arg., distributa nonnisi foliis basi vix attenuatis costa pilosis et floribus subsessilibus distingui possunt.

Croton (Sect. EUTROPIA Muell. Arg.; § Cyclostigma Griseb.) **verapazensis** Donn. Sm.—Folia petiolo longiora ovata sensim acuminata basi rotundata subquinquenervia utrinque sparsim stellato-pilosa. Petiolus apice stipitato-biglandulosus. Stipulae subulatae. Racemi distanter fasciculiflori, bracteis linearibus. Stamina circiter 15. Styli bis terve divisi.

Indumentum pilo centrali elongato stellatim pilosum in ramulis petiolis foliis nascentibus racemis calycibus ovariis ochraceo-tomentulosum. Folia membranacea utrinque viridia 8–10 cm. longa 5.5–7.5 cm. lata glandulis minutis denticulata, petiolo 3–4.5 cm. longo, stipulis primum setaceis denique validioribus 4 mm. longis. Racemi 12–13 cm. longi, bracteis cito deciduis 5 mm. longis, inferioribus flores femininos simulque masculinos, reliquis tantum masculinos, fulcientibus, pedicellis masculinis quam feminina parum longioribus 3–5 mm. longis. Calycis segmenta fere sejuncta oblongo-ovata, feminina 2.5 mm. longa masculinis paulo majora margine plana. Petala masculina oblongo-elliptica 2.5 mm. longa scariosa villosa, feminina rudimentaria setacea aegre 1 mm. longa. Stamina 12–18, filamentis fere glabris 3 mm. longis, antheris subquadratis 0.5 mm. longis. Discus masculinus villosus, glandulis remotis orbicularibus, femininus glandulis contiguis crenulatis circumdatus. Ovarium subglobosum 2 mm.-diametrale, stylis plerumque bis dichotome partitis. Capsula stellatim pubescens 1 cm. longa, seminibus 5 mm. longis fuscis leviter rugosis.—Ad *C. hemiargyrium* Muell. Arg. accedens.

Santa Rosa, Depart. Baja Verapaz, Guatemala, alt. 1600 m., Jul. 1908, *H. von Tuerckheim* n. II. 2297.

Croton (§ DREPADENIUM Muell. Arg.) **Tuerckheimii** Donn. Sm.—Folia coriacea nitida oblongo- vel obovato-elliptica acuminata basi obtusiuscula vel acuta penninervia denticulata. Flores masculini axillares racemosi. Calyx 6–12-lobatus, receptaculo explanato tubum fere implente toto glandifero. Stamina numerosissima.

Arbor formosa (cl. repertor in literis), omnibus in partibus glaberrima, ramulis petiolisque glandulosis, novellis complanatis glaucis. Folia alterna 7–9.5 cm. longa 3–4 cm. lata incurvo- vel cuspidato-acuminata margine cartilagineo revoluta glandulis remote minuteque denticulata, petiolo canaliculato 7–12 mm. longo. Pedunculus communis in axillis superioribus situs vix ullus vel usque ad 7 mm. longus, pedicellis 5–7 corymboso-subfasciculatis 7–14 mm. longis, bracteis bracteolisque scariosis semiamplexicaulibus obtuse ovatis 2–2.5 mm. longis, floribus tantum masculinis cognitis. Calycis lobi plerumque 8 cuspidato-ovati vel -triangulares parum aequales 1.5–2 mm. longi, receptaculo 4–6 mm. lato glandis compactis compresso-subcubicis 0.5 mm. longis obsito. Petala obsoleta. Stamina inter glandas inserta 60–85, filamentis 3–3.5 mm. longis, antheris ovalibus 1 mm. longis prope basin affixes. Flores feminini et fructus ignoti.

Apud pagum *Tactic* dictum, Depart. Alta Verapaz, Guatemala, alt. 1550 m., Mart. 1908, *H. von Tuerckheim* n. II. 2163.

Acalypha (§ ACROSTACHYAE Muell. Arg.) **radinostachya** Donn. Sm.—Dioica. Folia oblongo-ovata crenato-serrata 3-nervia. Stipulae lineari-lanceolatae perlonge setaceo-productae. Spica feminina gracilis longissima, bracteis dissitis unifloris deltoideo-ovatis subintegris. Styli toti numerosissime longissimeque lacinuligeri.

Suffrutex erectus vix metralis simplex, caule petiolis foliorum nervis spica bracteis sparsim minuteque strigillosis. Folia nascentia dense luteo-strigillosa, adulta glabrescentia tenuiter membranacea 13–14.5 cm. longa 7–8.5 cm. lata graciliter acuminata basi rotundata leviter retusa, suprema conferta, petiolo 2.5–4 cm. longo ad apicem glandulis binis oblongis 1 mm. longis instructo, stipulis seta 10 mm. longa computata 17 mm. longis. Spica solum feminina nota terminalis sessilis usque ad 32 cm. longa. Bracteae 2 mm. longae atque latae acuminatae utrinque glandulis stipitatis minute 2–3-denticulatae. Sepala 3 ovata acuta 1 mm. longa. Ovarium globosum sepala aequans cum illis parce strigillosum, stylis 2 mm. longis, quoque lacinulis circiter 20–25 capillaceis simplicibus usque ad 6 mm. longis albidis biseriatim pectinato. Cetera desunt.

In silvis primaevis profundis ad fundum *Suerre* dictum, Llanuras de Santa Clara, Comarca de Limón, Costa Rica, alt. 300 m., Febr. 1896, *John Donnell Smith*, n. 6849 ex Pl. Guat. etc. quas ed. Donn. Sm.

Conceveiba (§ VECONCIBEA Muell. Arg.) **pleiostemona** Donn. Sm.—Folia suborbicularia vel orbiculari-obovata abrupte cuspidata basi rotundata vel retusa. Pedicelli masculini singuli vel 2–4-ni inaequales medio articulati calycem nutantem subaequantes. Stamina circiter 50–60.

Ex scheda cl. repertoris arbuscula, ramulis stipulis petiolis foliorum utrinque nervis panicula stellatim griseo-pubescentibus. Folia nascentia densissime praesertim in nervis utrinque tomentulosa, adulta praeter nervos supra glabrescentia venis venulisque subtus stellatim puberula pergamentacea concoloria pellucida glandulari-denticulata penninervia 13.5–18 cm. longa, 10–13.5 cm. lata, cuspide 1 cm. longa obtusa, nervis lateralibus utrinsecus 5–6, venis transversis 3–4 mm. inter se distantibus, petiolo striato 5–7.5 cm. longo, stipulis subulatis 5–6 mm. longis persistentibus. Panicula ex solis speciminibus masculinis nota sessilis 12–18 cm. longa, ramis erecto-patentibus, pedicellis plerumque trinis 2–3 mm. longis, articulo inferiore tomentuloso, superiore nitido, bractea bracteolisque ovato-lanceolatis 1–2 mm. longis. Calyx nitidus globosus 2.5 mm.-diametralis 2–3-partitus, segmentis demum reflexis. Stamina omnia antherifera conformia, filamentis glabris 7–11 mm. longis, antheris ob loculos late separatos latioribus quam longioribus. Flores feminini fructusque deficientes.—Affinitas cum *C. latifolia* Benth. summa est.

Ad ripas Río Blanco in fundo *Rosario* dicto, Llanuras de Santa Clara, Comarca de Limón, Costa Rica, alt. 300 m., Jul. 1899, *H. Pittier* n. 13425.

F63-312

Ampelocera hondurensis Donn. Sm.—Aculeata. Folia integerrima obovato-elliptica obtusiuscula basi cuneata. Paniculae foliis 2–3-plo breviores. Perianthium quinquefidum, segmentis obovatis integris. Stamina 11–14, antheris in alabastro reversis. Ovarium ellipsoideum stylis subtriplo superatum.

Arbuscula (cl. repertor in scheda), omnibus in partibus glabra cortice griseo lenticellata spinis axillaribus rectis 5–11 mm. longis armata. Folia subcoriacea nitida 8–12 cm. longa 3.5–5 cm. lata a basi penninervia, nervis lateralibus late patulis utrinque 8–10, petiolo 4–8 mm. longo. Paniculae utriusque sexus in ramulis distinctis sitae a basi erecto-patenter ramosae 4–6 cm. longae densiflorae siccitate nigricantes, pedicellis late patentibus basi et medio minute bracteolatis prope florem articulatis, masculinis 2 mm. longis quam feminini dimidio brevioribus. Perianthii segmenta nigro-punctulata et -lineolata concava valde imbricata margine scariosa 2–3 mm. longa, masculina femininis paulo latiora. Stamina circiter 12, filamentis confertis capillaceis 2 mm. longis, antheris demum erectis oblongis 1.5 mm. longis. Ovarium 2 mm. longum, stylis 5–7 mm. longis, ovulo orbiculari complanato. Drupa ignota.—Haec species in genere tertia ad *A. Ruizii* Klotzsch perianthio 5-fido ad *A. cubensem* Griseb. foliis integris accedens, ab utraque inter alia spinis inflorescentia perianthii segmentis integris staminibus indefinitis antheris primum reversis recedit.

Secus viam prope San Pedro Sula, Depart. Santa Bárbara, Honduras, alt. 200 m., Maj. 1890, *Carl Thieme*, n. 5606 ex Pl. Guat. etc. quas ed. Donn. Sm.

BALTIMORE, MD.

INFLUENCE OF PHOSPHATE ON THE TOXIC ACTION OF CUMARIN[1]

J. J. Skinner

In connection with a study of the different effects produced as the result of the action of several organic compounds on seedling wheat, presented in a former paper,[2] it was noted that the presence of phosphate in the nutrient solutions employed was able to minimize or entirely overcome the toxic effect of the cumarin on the seedlings. The effects of the cumarin on plant development are strikingly shown on the seedling wheat. The leaves are shorter and broader than is normal for wheat, and only the first leaves are usually unfolded, the other leaves remaining wholly or partially within the swollen sheath; such leaves as do break forth are usually distorted and curled or twisted. The disappearance of this characteristic behavior of the cumarin affected plants was, therefore, an additional criterion of the beneficial effect of the phosphate in the nutrient cultures, as well as the improved growth and better root development of the plants in general. The nutrient solutions contained nitrate as sodium nitrate, potassium as potassium sulphate, and the phosphate was added in the form of monocalcium phosphate.

Attention was called in the earlier paper to the fact that the observation there recorded was obtained with the calcium acid phosphate, and that the observed result may be caused, therefore, by the salt as a whole rather than by the phosphate radical contained therein, or by other specific qualities of the salt or other constituent parts, namely by its acid properties or the fact that calcium is present in the compound.

Several experiments were planned so as to eliminate the possibility of calcium producing the result noted, and to present the

[1] Published by permission of the Secretary of Agriculture.

[2] Schreiner, O., and Skinner, J. J., The toxic action of organic compounds as modified by fertilizer salts. Bot. Gaz. **54**:31–48. 1912.

phosphate under different conditions, acid, neutral, and alkaline. These requirements are met by using sodium salts instead of calcium, and employing all three sodium salts of phosphoric acid, namely, the monosodium phosphate (NaH_2PO_4), which like the calcium acid phosphate of the first experiment is decidedly acid in reaction; the disodium phosphate (Na_2HPO_4), which is neutral toward phenolphthalein; and the tribasic sodium phosphate (Na_3PO_4), which is alkaline in reaction. In all other respects the culture solutions were the same in concentration and composition as described in the earlier paper, the full number of 66 cultures as there described being used, both with and without the cumarin and, as in the paper cited, comparisons are always made between solutions of like composition as far as the mineral salts are concerned. This comparison, of course, can be made between individual cultures of like composition or between groups of cultures, when members of like composition occur in both groups.

Effect of monosodium phosphate

The 66 culture solutions of equal concentration (80 p.p.m. of $P_2O_5+K_2O+NH_3$), but varying in composition as far as the ratios of phosphate, potash, and nitrate are concerned, were prepared according to the scheme presented in the earlier paper cited. The sets were always in duplicate, the one containing only the nutrient salts and considered as the normal set, the other containing in addition to the salts 10 p.p.m. of cumarin. The plants grew from October 17 to 29. The green weight at the termination of the experiment for the growth in the 21 cultures composed of mainly phosphatic fertilizer (one-half and more of the nutrients being phosphate) was 38.6 grams. Similarly the green weight of the cultures composed of mainly nitrogenous fertilizer was 42.0 grams, and in the cultures composed mainly of potassic fertilizers it was 41.8 grams. The results in the normal set were: for the mainly phosphatic fertilizers, 39.3 grams; for the mainly nitrogenous fertilizers, 49.9 grams; for the mainly potassic fertilizers, 46.9 grams. These results are tabulated in table I, which also gives the results relatively expressed in terms of the normal culture taken as 100.

It will be seen that the mainly phosphatic cultures gave a growth in the presence of cumarin which was nearly as good as in the cultures without cumarin. The growth relatively expressed was 98 per cent of the normal. With the other groups it was 84 and 89 per cent. The result with the monosodium phosphate is therefore similar to the action of the monocalcium phosphate reported in the earlier paper, a fact which is also shown by the appearance of the plants in the cultures composed of mainly phosphatic fertilizers, the plants having lost entirely the characteristic effect of the cumarin above referred to, an effect which is

TABLE I

SHOWING THE EFFECT OF THE MAINLY PHOSPHATIC, MAINLY NITROGENOUS, AND MAINLY POTASSIC FERTILIZERS ON CUMARIN

Phosphate as monosodium phosphate

FERTILIZERS COMPOSED OF 50 TO 100 PER CENT OF	GREEN WEIGHT		RELATIVE GROWTH (NORMAL =100)
	Normal	With 10 p.p.m. cumarin	
	grams	grams	
Phosphate	39.3	38.6	98
Nitrate	49.9	42.0	84
Potash	46.9	41.8	89

strongly marked in the cultures low in monosodium phosphate as well as in those low in calcium acid phosphate. This experiment, therefore, disposes quite effectively of the supposition that the calcium in the phosphate salt played any significant part in the observed action, since the same action in all particulars is possessed by the monosodium phosphate. There remains the question of the influence or action of the acid character of both phosphates in bringing about the observed result. For this purpose culture experiments in which the acid phosphates were replaced by neutral and even alkaline phosphates were made.

Effect of disodium phosphate

The plants in this experiment grew from November 1 to 12, and the results are presented in table II, the grouping being again made on the basis of the composition of the nutrient salts in the

cultures, that is, into the groups mainly phosphatic, mainly nitrogenous, and mainly potassic.

TABLE II

SHOWING THE EFFECT OF THE MAINLY PHOSPHATIC, MAINLY NITROGENOUS, AND MAINLY POTASSIC FERTILIZERS ON CUMARIN

Phosphate as disodium phosphate

FERTILIZERS COMPOSED OF 50 TO 100 PER CENT OF	GREEN WEIGHT		RELATIVE GROWTH (NORMAL =100)
	Normal	With 10 p.p.m. cumarin	
	grams	grams	
Phosphate	36.3	34.1	94
Nitrate	45.8	40.3	88
Potash	44.5	38.2	86

Here again the effect of the mainly phosphatic fertilizers is the same as with the monobasic salts already discussed, although this effect is not as marked in this experiment. There remains the trisodium phosphate of alkaline reaction to be studied in this regard.

Effect of trisodium phosphate

The plants in this experiment grew from November 29 to December 10 and the results are given in table III.

TABLE III

SHOWING THE EFFECT OF THE MAINLY PHOSPHATIC, MAINLY NITROGENOUS, AND MAINLY POTASSIC FERTILIZERS ON CUMARIN

Phosphate as trisodium phosphate

FERTILIZERS COMPOSED OF 50 TO 100 PER CENT OF	GREEN WEIGHT		RELATIVE GROWTH (NORMAL =100)
	Normal	With 10 p.p.m. cumarin	
	grams	grams	
Phosphate	37.0	33.9	91
Nitrate	42.4	34.6	81
Potash	42.9	31.7	74

These figures show that the effect of this alkaline reacting tribasic phosphate has the same effect in overcoming the toxic action of the cumarin as had the calcium acid phosphate, the

monosodium phosphate, and the disodium phosphate. The reaction of these various phosphates, and probably also the presence of the calcium, appears to modify this action, as indicated by the different figures, but it in nowise determines the effect itself. The conclusion seems warranted that the peculiar action of these phosphate salts in overcoming the toxic action of cumarin is due to the phosphate radical and not to the presence of any particular base, or the acid or alkaline reaction of the nutrient solution.

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BUREAU OF SOILS
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BRIEFER ARTICLES

ABSORPTION OF BARIUM CHLORIDE BY ARAGALLUS LAMBERTI[1]

During the progress of some experimental work on loco plants at Hugo, Colorado, we were led to suppose that these legumes contained much more barium salts than other plants growing in the same localities, and presumably possessed some qualities which enabled them to withdraw more of these salts from the soil. The question arose whether an increase of the quantity of barium in the soil would be followed by a corresponding increase in the plants, and to this end a series of experiments was undertaken. These experiments were not carried out as a complete study of the question, and were discontinued after the facts were obtained which had an immediate bearing on the problems which were under consideration. While the work was only preliminary in character, the results obtained may be of interest to others, and inasmuch as this work will not be continued, it may be best to publish the facts for the use of those who may be studying similar problems. While the general plan of the experiment was outlined by the writer, the detail was carried out by Assistant HADLEIGH MARSH. A plot of ground was selected on the ranch of Mr. OLSON, near Hugo, where *Aragallus Lamberti* grew with especial luxuriance. This plot was fenced in order that grazing animals might not interfere with the progress of the experiment.

EXPERIMENT NO. 1

Six thrifty plants of *Aragallus Lamberti* were selected for barium chloride treatment, and 7 plants, somewhat smaller, were selected for a control by treatment with an equal amount of water. A shallow trench was dug around each plant. These trenches were filled daily with barium chloride solution in the case of the plants experimented upon, and with an equal quantity of water in the case of the control plants. The barium chloride was applied in a 10 per cent solution. The solution was made with water containing some sulphates, so that there was a slight precipitation of sulphate of barium when the solution was made, but it is not

[1] Published by permission of the Secretary of Agriculture.

to be presumed that this made any material difference with the amount of barium chloride in solution. Two liters of barium chloride solution were applied to each of the experimental plants daily. The 10 per cent solution was used from July 8 to July 11, 1908, inclusive. On July 13, 5.5 per cent solution of barium chloride was used. No more of the solution was applied, and on July 18 it was found that the plants treated with barium chloride solution had turned yellow and dried up, while those treated with water were still green and fresh. The grass which surrounded the trenches did not seem to be affected by the barium chloride solution. Both sets of plants were dug and dried for chemical analysis.

Unfortunately the plants treated with water were by mistake thrown away, so that no analysis could be made. However, an analysis was made of *Aragallus Lamberti* collected on the tract adjacent to the fenced patch at about the time when this experiment was going on, and this will serve as a basis of comparison, though not having the value of an analysis of the control plants. The analyses were made by the Bureau of Chemistry. The plants treated with barium chloride showed ash 41.08 per cent and barium 1.32 per cent. The *Aragallus Lamberti* collected in the area adjacent to the experimental plot showed ash 22.08 per cent and barium 0.106 per cent.

EXPERIMENT NO. 2

Inasmuch as it was shown that a 10 per cent solution of barium chloride was poisonous to *Aragallus Lamberti*, it was decided to use a very much more dilute solution and to duplicate the preceding experiment, using a 0.1 per cent solution.

In this experiment 9 plants were chosen for the barium chloride treatment, and 9 similar plants for the control experiment with water. Sixteen liters of barium chloride solution were used daily on the experimental plants, and 16 liters of water on the control plants, with the exception of one day when 14 liters were used. This experiment was carried on from August 4 to August 18, inclusive. During this time both groups of plants continued healthy and showed no effect of the treatment. On August 20 both sets of plants were dug up and dried for analysis, these analyses, as in the other cases, being made by the Bureau of Chemistry. The plants treated with barium chloride showed ash 52.26 per cent and barium 0.20 per cent. The plants treated with water showed ash 22.98 per cent and barium 0.0613 per cent.

EXPERIMENT NO. 3

In the third experiment, the barium chloride was used in a 1 per cent solution. As in the preceding experiments, one group of plants was watered with the barium chloride solution and the other with an equal amount of water. Sixteen liters of the barium chloride solution and of water, respectively, were used daily in this experiment. This was commenced on September 15, and was continued to September 21, inclusive. At this time both groups of plants were in good condition, showing no ill effects from the treatment. On September 22 the plants were dug up and dried for analysis. The analyses, made by the Bureau of Chemistry, showed the following results: the plants treated with barium chloride, ash 37.095 per cent, barium 0.636 per cent. The plants treated with water showed no barium.

RESULTS

These preliminary experiments appear to show the following results: That plants of *Aragallus Lamberti* endure barium chloride solution as strong as 1 per cent with no bad effects, while a 10 per cent solution is distinctly poisonous. Grouping the analyses, we find that the largest amount of barium was found in those that were treated with the 10 per cent solution, a less amount in those treated with the 1 per cent solution, and a still less in those receiving the 0.1 per cent solution. In other words, it appears that in these experiments the quantity of barium salts absorbed varied directly with the amount in the soil.—C. DWIGHT MARSH, *Bureau of Plant Industry, U.S. Department of Agriculture.*

CURRENT LITERATURE

BOOK REVIEWS

Lotsy's textbook

The first part of the third volume of LOTSY's *Vorträge über botanische Stammesgeschichte*[1] begins with the Coniferae and ends with Casuarinaceae. There are 1055 pages and 661 figures, scarcely any of which are original. The principal literature, especially the morphological, is gathered together and illustrations are lavishly reproduced, often whole plates, rather than merely the figures bearing upon the subject. In the case of such an extensive work it would be impossible to give any lengthy summary or to discuss even the principal conclusions, but a few points might be noted.

In concluding the 286 pages devoted to Coniferae, he finds that the phylogeny is still uncertain, but that they must have come from the great Filicales complex, and that they contain forms in which the ovulate structures should be called a flower and others in which they constitute an inflorescence; consequently, those who are convinced that the angiosperms have come from the Coniferae are at liberty to regard the angiosperm flower as either a strobilus or an inflorescence. LOTSY continues in his previous belief that the Gnetales have not given rise to the angiosperms, but rather represent the end of an evolutionary line.

The monocotyledons, with the exception of the Spadiciflorae, which LOTSY places near the Piperales, form a consistent group, and have been derived from the dicotyledons. The Alismaceae are regarded as the most primitive family and the Orchidaceae as the most advanced. The various families are considered seriatim, and their external habit and internal morphology are well illustrated, but there is little effort to show general tendencies.

Attention may also be called to a few details. In considering Gnetales, COULTER'S interpretation of the tissue at the base of the free nuclear embryo sac is questioned, but no new evidence is introduced. In the opinion of the reviewer, COULTER'S interpretation is correct and LOTSY'S own preparations would show the boundary of the embryo sac between the free nuclear portion and the so-called antipodal region.

Miss PACE'S interpretation of the embryo sac of *Cypripedium* is also questioned, LOTSY regarding the two cells resulting from the first division of the

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[1] LOTSY, J. P., Vorträge über botanische Stammesgeschichte, gehalten an der Reichsuniversität zu Leiden; ein Lehrbuch der Pflanzensystematik. Dritter Band: Cormophyta Siphonogamia. Erster Teil. 8vo. pp. 1055. *figs. 661*. Jena: Gustav Fischer. 1911. *M* 7.14.

megaspore mother cell as two megaspores. This is a surprising conception of the megaspore, for it would mean that a megaspore (and presumably a microspore) could be formed with only one of the reduction divisions, that is, the megaspore would be completely formed at the close of the heterotypic mitosis. Cytologists will hardly accept such an interpretation.

The angiosperm embryo sac is interpreted as consisting of micropylar and an antipodal archegonium. This is another view which can hardly be accepted by one who has followed the gradual reduction of the female gametophyte from the bryophytes to the spermatophytes.

The book brings together an immense amount of material and will be useful just as an encyclopedia is useful. In such voluminous publications originality is not to be expected. There is a general index and an index of plant names. Many references to literature are given in the text, but the complete bibliography will be deferred until the work is complete.—CHARLES J. CHAMBERLAIN.

MINOR NOTICES

Forestry in Indiana.—The annual report of the Indiana State Board of Forestry[2] for the past year contains two papers of more than usual interest. The shorter, by STANLEY COULTER, contains a valuable mass of data on the rate of growth of various native tree species found upon the state reservation. Its study should make the selection of the best species for forest planting an easier matter, while at the same time it serves to emphasize the importance of conserving what has been the product of centuries of plant activity.

The longer article, by C. C. DEAM, the secretary of the board, is an illustrated descriptive list of the tree species native to the state and occupies 270 pages of the report. Excellent botanical descriptions of some 125 species are supplemented by full-page drawings of leaves and fruit, together with notes upon the economic uses and horticultural value of the trees, making it a valuable handbook of the forests of the state.—GEO. D. FULLER.

NOTES FOR STUDENTS

Recent work among gymnosperms.—STILES[3] has investigated some material of *Podocarpus*, *Dacrydium*, and *Microcachrys*, and has made it the basis of a synthetic presentation of the classification, morphology, history, and phylogenetic connections of the group. The bringing together of this wealth of details in an organized form will serve the very useful purpose not only of suggesting genetic connections but also of indicating the important gaps in our knowledge. The general features of the group are summarized clearly and compactly under the categories of vegetative organs, spore-producing

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[2] Eleventh annual report of Indiana State Board of Forestry for the year 1911. pp. 372. *pls. 133*. Indianapolis: Wm. B. Burford. 1912.

[3] STILES, WALTER, The Podocarpeae. Ann. Botany **26**:443–514. *figs. 8. pls. 46–48*. 1912.

members, and gametophytes. The most interesting feature of every such review of all the available knowledge in reference to a group is the conclusion as to its phylogenetic connections. In this case it is said that "the Podocarpeae are probably related to the Araucarieae, and, though to a much less extent, to the Abietineae." These connections have certainly long been obvious, as well as the absence of any evidence of a close connection with the Taxeae. The following statement, however, is not so obvious: "A consideration of the available evidence shows that there is much to be said for the view that regards the Coniferales as descendants of paleozoic lycopodialean ancestors." Much may be said for this view, but none of it seems convincing.

GIBBS[4] has studied the development of the "female strobilus" of *Podocarpus*, a structure that certainly needs elucidation. It seems that the difficulties of interpretation disappear when the early stages of the strobilus are studied, thus eliminating the confusion of secondary modifications. Such a study "strikingly reveals the relationship of the axis to the strobilus or cone of Abietineae and its component parts." This includes the conclusion that the "ovuliferous envelope" of the podocarps is the equivalent of the ovuliferous scale of the Abietineae, which fuses "more and more till finally it merges in the ovular integument in *Torreya* and *Cephalotaxus*." The reduction in the strobilus organization is traced from Abietineae, through *Microcachrys* and *Dacrydium*, until it reaches its extreme expression in *Podocarpus*, in which genus, therefore, we are dealing with a much modified cone. Many details of structure are given which add materially to our knowledge of this interesting genus.

STILES[5] published a brief note on the gametophytes of *Dacrydium* before the appearance of his comprehensive paper on the podocarps noted above. The details given emphasize the resemblance of the male gametophyte to those of *Podocarpus* and *Phyllocladus*, and the closer resemblance of the female gametophyte to that of *Phyllocladus* than to that of *Podocarpus*. It is becoming increasingly evident that *Phyllocladus* is a podocarp rather than a taxad.

Miss DUTHIE[6] has investigated the anatomy of *Gnetum africanum*, a climbing species. Details are given of the structure of xylem, phloem, pith, medullary rays, cortex, latex tubes, epidermis of stem, cork, and leaves.

PEARSON[7] has investigated three species of *Gnetum* (*G. scandens*, *G. africanum*, and *G. Buchholzianum*), the study of the microsporangium and

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[4] GIBBS, L. S., On the development of the female strobilus in *Podocarpus*. Ann. Botany **26**:515–571. *pls. 49–53*. 1912.

[5] STILES, WALTER, A note on the gametophytes of *Dacrydium*. New Phytol. **10**: 342–347. *figs. 4*. 1911.

[6] DUTHIE, AUGUSTA V., Anatomy of *Gnetum africanum*. Ann. Botany **26**:593–602. *pls. 57–59*. 1912.

[7] PEARSON, H. H. W., On the microsporangium and microspore of *Gnetum*, with some notes on the structure of the inflorescence. Ann. Botany **26**:603–620. *figs. 6*. *pls. 60, 61*. 1912.

microspore being chiefly those of *G. africanum*. The inflorescence is described and also the details of spermatogenesis from the mother cell to the microspore, the reduced number of chromosomes being 12. Great interest attaches to the male gametophyte of *Gnetum*, but the present account does not clear it up. At pollination, three free nuclei were observed in the pollen grain, which "are probably to be identified as one prothallial, one vegetative (tube), and one generative." Since LOTSY has figured three free nuclei in the pollen tube of *Gnetum Gnemon*, which were obviously a tube nucleus and two male cells, the free "prothallial nucleus" in the pollen grain is open to doubt. One would like to be sure whether *Gnetum* has eliminated prothallial tissue or not. The author says that "the germination of the microspore and the structure of the pollen grain point to a much closer degree of affinity with *Welwitschia* than with *Ephedra*," a conclusion which all other structures confirm.

Miss GORDON[8] has discovered ray tracheids, both marginal and interspersed, in old stem wood of *Sequoia sempervirens*. Since the wood of this form is primitive enough in features to suggest its comparison with root wood, the presence of ray tracheids is especially interesting.

WIELAND[9] has published an interesting account of *Williamsonia*, a genus which he has done so much to elucidate. A few years ago a problematical genus, it has now emerged clearly as a prominent Mesozoic group. An account is given of its discovery, its structure, and its phylogenetic connections. Its great range in habit, its variations in the structure of the strobilus, its variable foliage, all suggest wide relationships, and among these suggested relationships WIELAND sees emphasized his contention that the angiosperms have been derived from the Bennettitales.

The same author,[10] in continuing his studies on the trunks of *Cycadeoidea*, has discovered that some of the supposed young strobili are mature ones of reduced type. This incidentally disturbs some of the previous conclusions as to relationships among the species of *Cycadeoidea*, and especially extends our knowledge as to the range of variation in the structure of the strobilus. These reduced or simplified forms of course are more suggestive of the structure of the angiosperm flower.—J. M. C.

Inheritance of doubleness in stocks.—Doubleness in stocks (*Matthiola*) presents one of the most complicated cases of inheritance yet thoroughly studied, but Miss SAUNDERS[11] has developed á scheme which allows a consistent

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[8] GORDON, MARJORIE, Ray tracheids in *Sequoia sempervirens*. New Phytol. **11**:1–7. *figs. 7.* 1912.

[9] WIELAND, G. R., On the Williamsonian tribe. Amer. Jour. Sci. **32**:433–466. *figs. 18.* 1911.

[10] WIELAND, G. R., A study of some American fossil cycads. Part VI. On the smaller flower-buds of *Cycadeoidea*. Amer. Jour. Sci. **33**:73–91. *figs. 11.* 1912.

[11] SAUNDERS, Miss E. R., Further experiments on the inheritance of "doubleness" and other characters in stocks. Jour. Genetics **1**:303–376. *pls. 2. figs. 2.* 1911.

and orderly presentation of most of the facts brought to light by extensive cultures, and by means of which the results to be secured from any particular mating is capable of prediction with a fair degree of accuracy. Double stocks are totally sterile and must always be derived from singles, either self-fertilized or crossed with other singles. Single stocks are of two kinds with respect to their relation to doubleness, namely, "*no-d*-singles" which breed true to singleness when selfed or crossed with others of their own kind, and "*d*-singles" which when similarly bred always produce both singles and doubles, the doubles being generally in excess of the singles. Reciprocal crosses between *d*-singles and *no-d*-singles give unlike results, owing apparently to a difference in the genotypic constitution of eggs and sperms in the *d*-singles, the eggs being of two sorts while the sperms are all equal. Doubleness is recessive and disappears in the F_1, but when the *d*-single is the seed-parent the F_1 singles are of two sorts, some breeding true to singleness, others producing both singles and doubles. When the *d*-single is the pollen-parent, the F_1 singles are all of one kind and all give both singles and doubles in F_2. The ratios of singles to doubles in the pure-bred *d*-single race have always been suggestively near 7:9, thus indicating that the difference between singles and doubles involves two genes instead of one.

Miss SAUNDERS assumes that singleness is due to the presence of two factors *X* and *Y*, the absence of one or both of these resulting in doubleness. If these two factors were independent, the expected ratio would be 9 singles to 7 doubles, but if they are coupled according to the scheme discovered in sweet peas, etc., $n-1:1:1:n-1$, the doubles would be in excess of the singles as observed. The experimental results accord well with this assumption, and make it probable that the coupling is of the form 15:1:1:15, though possibly 7:1:1:7. The peculiar feature in stocks, however, as compared with the coupling in sweet peas, is the fact that neither *X* nor *Y* are carried by the pollen, and the coupling can show itself only in the constitution of the eggs. The crosses with *no-d*-singles resulted in an unexpectedly small number of doubles in F_2, owing, as proved by further breeding, to the fact that in the *no-d*-single race singleness is not produced by the joint action of *X* and *Y*, but of a similarly coupled pair *X'* and *Y'*. To further complicate the situation, there occurs a "sulfur-white" *d*-single race in which the plastid-color is also "eversporting" in a manner quite similar to doubleness, the pure-bred progenies always consisting of whites and creams as well as doubles and singles, the singles being all white, the doubles mostly cream but also sometimes white. The white plastids are assumed to be due to a factor *W* which is borne by only a part of the eggs and by none of the sperms. Moreover *W* is coupled with one of the factors for singleness, either *X* or *Y*. Although in the pure *d*-single strains *X*, *Y*, and *W* are carried only by the eggs, crosses between *d*-singles and *no-d*-singles of different plastid-color produced heterozygous F_1 plants in which both pollen and eggs carried the coupled series of genes.

In an appendix the author shows that the increase in proportion of doubles derivable from old seed is due to the greater longevity of the seeds which lack *X* and *Y*, and not to any change in the genotypic nature of any single seed. She also tried to separate singles and doubles on the basis of seed-characters, but was able to do this only in the sulfur-white race, and then not by the character for doubleness, but by the white or cream plastid-color, which as stated above proved to be coupled with one of the factors for singleness. Ten-week stocks are much branched and the Brompton stocks unbranched. The unbranched condition is recessive, but the ratio is somewhat modified because typically unbranched plants will develop some branches when the terminal bud is injured. Notes are also appended regarding the inheritance of several sap-colors, rose, lilac, terra-cotta, carmine, and crimson.—GEO. H. SHULL.

Biology and taxonomy of Gymnosporangium.—A monograph treating of *Gymnosporangium* both in its biological and its taxonomic aspects is the outcome of several years of experimental and observational work on that genus by KERN.[12] The work is divided into two parts, the first dealing with the biology and the second with the taxonomy of the genus.

In Part I the biology of the genus is discussed under the following general heads: Introduction (including the life history, general characteristics, and nuclear phenomena), distribution and relationships, experimental investigations of life histories, and pathological and economic importance. Particular attention is given to the geographical distribution of the species with reference to the distribution of their hosts. The main facts are arranged in convenient tables. The forms associated with the two sections of *Juniperus* present the most interesting features in regard to their distribution. The species which occur on the section *Sabina* belong either exclusively to the western or exclusively to the eastern hemisphere, while of those occurring on species of the section *Oxycedrus* some are common to both hemispheres and others are limited to one hemisphere. These facts lead the author to the conclusion that the forms found on the older section (*Oxycedrus*), some of whose species are distributed over all the continents of the northern hemisphere, were distributed with their hosts "during a geological period when the land conditions permitted migrations between the northern continents." The author supposes that the section *Sabina* has developed from the section *Oxycedrus* since the continents have become isolated, therefore "we would not expect to find the same species, either of hosts or fungi, indigenous in North America and in the Old World; and this, indeed, is the case." This view of course implies the independent origin of species of the section *Sabina* in the two hemispheres.

Regarding the limited geographical distribution of species of *Gymnosporangium* in cases where both the hosts have a wider distribution, no satis-

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[12] KERN, FRANK DUNN, A biologic and taxonomic study of the genus *Gymnosporangium*. Bull. N.Y. Bot. Gard. 7:392–494. 1911.

factory conclusions can be deduced from the data at hand. The apparently limited distribution of the fungus may merely indicate a scarcity of collections. A table indicating distribution of the species shows in general that the teleutospore generation is more restricted as to its hosts than the aecidial generation. Only 4 genera (5 if the two sections of *Juniperus* are considered as genera) serve for hosts of teleutospores, while 15 genera serve as aecidial hosts, *Crataegus* and *Amelanchier* being in the lead among these. While the aecidial generation has always been regarded as confined to the *Pomeae*, the work of recent years has shown that one form has aecidia on *Gillenia* (*Porteranthus*) of the Spiraeeae, and another on *Fendlera* and *Philadelphus* of the Saxifragaceae, while *G. bermudianum* is autoecious.

Part II comprises the systematic treatment of the genus, 40 species being recognized and described, the descriptions being in most cases accompanied by figures of spores or peridial cells showing characteristic features. Of the 40 species known in the world, 29 are known in their complete life cycle, 7 are known only in their aecidial phase, and 4 only in their telial phase. *Gymnosporangium fraternum*, *G. juvenescens*, and *G. effusum* are described as new, and the aecidial hosts of three species are reported for the first time. The taxonomic treatment is preceded by two sets of keys based respectively on the characteristics of the fungus and on those of the hosts. Most of the species are admirably illustrated by halftone plates.—H. HASSELBRING.

Inheritance of root-form and color in beets and turnips.—The large number of varieties of beets and turnips characterized by distinctive forms and colors of the roots has long invited the attention of experimental breeders, but the very abundance of material has doubtless acted as a deterrent to genetic investigation. KAJANUS[13] has undertaken the difficult task of analysis. As a first approximation to a complete solution of hereditary form-relations in beets, he finds the probable existence of six independent genes affecting the form, namely, two genes (L_1 and L_2) which produce an elongation of the roots, two (A_1 and A_2) which cause the roots to be taper-pointed below, an inhibitor (B) which opposes the action of the elongation-genes, and another (O) which opposes the action of the taper-point genes. When B and O are not present, the long and tapered forms are epistatic over the short and blunt forms, but when these inhibitors are present, the apparent dominance is reversed. The evidence for the existence of these genes consists at present wholly in the occurrence of the ratios 3:1, 15:1, and 1:3 in the F_2. In most of the reported crosses the results run fairly close to these ratios, but

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[13] KAJANUS, B., Genetische Studien an *Beta*. Zeitschr. Ind. Abst. Vererb. **6**: 137–179. *pls. 9. figs. 2.* 1911.

———, Mendelistische Studien an Rüben. Fühlings Landwirthsch. Zeitg. **61**: 142–149. 1912.

———, Genetische Studien an *Brassica*. Zeitschr. Ind. Abst. Vererb. **6**: 217–237. *pls. 4.* 1912.

when so many determiners affect the same character, the F_2 ratios are only suggestive and not decisive. Until a third and perhaps still later generations have been grown, the assumptions made by the author remain hypothetical, but with the weight of the observed F_2 ratios in their favor. In the Brassicas studied, the situation appears to be much simpler. In the turnip-rooted cabbages or Swedes (*B. Napus*) the roots are always approximately globular, but in the turnips (*B. Rapa*) both globular and elongated forms occur and there appear to be, just as in beets, two elongation genes (L_1 and L_2). Here again the evidence for these two genes is the appearance of the long and round forms in the F_2 in the ratio 15:1, and a later generation must decide the correctness of the interpretation.

In regard to the color of the roots the situation is also quite complex, perhaps even more so than in respect to form. Red is in some cases dominant to its absence, in other cases recessive (owing probably to the presence of an inhibitor), and it may appear in crosses between two whites, white and yellow, rose and yellow, etc., showing its compound nature. Some of the color-ratios are approximately 15:1 and others 3:1, which are also interpreted as indicating the existence of more than one gene capable of producing independently the same color-character. In turnips the upper portion of the roots is red, green, or yellow, each of these colors being epistatic to those following. The lower portion of the roots is white or yellow, having the same color as the flesh, the white being epistatic to yellow. In the turnip-rooted cabbages the heads are either violet-red or green. There are two independent genes which produce violet-red pigmentation, the one giving a light red, the other a dark red. As the latter is completely epistatic over the lighter color, a cross in which both of these genes and their absence are involved, produces an F_2 progeny consisting of dark red, light red, and white, in the ratio 12:3:1. Both in form and color the heterozygotes are often intermediate, so that a more or less completely continuous series of forms is produced, thus making the analysis difficult. This fact makes very important the promised continuation of the work.—GEO. H. SHULL.

Inheritance in wheat.—NILSSON-EHLE[14] gives a further report on his long-continued experiments in the crossing of wheat varieties, dealing this time especially with the density of the spikes and resistance to yellow rust (*Puccinia glumarum*). Both of these characters are lacking in the definiteness which has made the study of many alternative characters easy and the results clear-cut and decisive, but the author's earlier demonstration of several independent genes producing the same apparent character in seed-color of wheat and in the awns of oats has given a key to these more difficult cases. The density of the spikes is apparently modified by three distinct genes, two of which (L_1 and L_2)

[14] NILSSON-EHLE, H., Kreuzungsuntersuchungen an Hafer und Weizen. II. Lunds Universitets Årsskrift. **7**:no. 6. pp. 84. 1911.

promote elongation of the heads, while the third (*C*) acts as an inhibitor which checks the longitudinal development of the heads. When all of these factors are absent, a moderately dense head results, as exemplified by the "squarehead" varieties. When *C* is present and both L_1 and L_2 are absent, the extremely dense "compactum" form is produced. Although considerable transgressive fluctuation renders the analysis doubtful in individual cases, the total result is sufficiently decisive to leave little doubt of the essential correctness of the interpretations. The discovery that several genes may affect quantitatively the same external characteristic has given an explanation of some hybrid progenies which have seemed to breed true to characters intermediate between the parents, and it also explains the intensification of parental characters in F_2 individuals which have often been observed. As an example of the latter phenomenon, a cross between two wheats of intermediate density, having the formulae CL_1L_2 and cl_1l_2, produces some F_2 plants with very dense heads (Cl_1l_2), and some with very lax ones (cL_1L_2). In respect to rust-resistance, the difficulties of analysis are still greater and the author makes no attempt to identify particular genes, but the results of a large number of tests in second and third generations show very clearly two important facts, namely, that there is a segregation of different grades of resistance in the F_2, and that the matter is not generally as simple as BIFFEN found it to be in his crosses dealing with this problem. In none of NILSSON-EHLE's crosses was there an indication of a simple monohybrid ratio (3:1) for rust-resistance, as was found by BIFFEN.

KAJANUS[15] reports an instance in which the *spelta*-character (zigzag rachis and adherent glumes) is recessive to the *vulgare*-character (straight rachis and free glumes), a situation exactly the reverse of that found by von TSCHERMAK. This indicates that there are two genotypes of one or the other of these two phenotypes, thus paralleling the now frequently demonstrated existence of dominant and recessive whites. KAJANUS found presence of awns recessive to their absence, and hairiness of the glumes dominant to its absence, as in all other reported crosses in which these characters have been involved. —GEO. H. SHULL.

Cytology and sexuality of Olpidiopsis.—Overcoming considerable difficulties in the matter of obtaining and managing material, BARRETT[16] has greatly increased our knowledge of the cytology and especially of the sexuality of the submerse chytrids. Three species of *Olpidiopsis*, parasitic on *Saprolegnia* and *Aphanomyces*, were studied, two of which (*O. vexans* and *O. luxurians*) are described as new. The first part of the paper consists of biological observations, among which will be found many valuable suggestions to anyone undertaking similar work. The zoospores are shown to have two equal flagella

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[15] KAJANUS, B., Zur Genetik des Weizens. Botaniska Notiser 1911: 293–296.

[16] BARRETT, J. T., Development and sexuality of some species of *Olpidiopsis* (Cornu) Fischer. Ann. Botany **26:** 209–238. *pls. 23–26.* 1912.

springing from the same point, although one is directed backward and sidewise in such a manner as to give the appearance of the short lateral cilium that has hitherto figured in the descriptions of this and some other genera of biflagellate Archimycetes. They are distinctly diplanetic and show a pulsating vacuole during the interval between the two periods of activity. Soon after infection the young parasites are lost to view in the host protoplasm, but retain their individuality and develop into zoosporangia without fusing to form plasmodia.

The parasite becomes coenocytic by nuclear division on the beginning of growth. The nuclei, which show the complete concentration of the chromatin into the karyosome characteristic of most chytridiaceous nuclei, appear to divide exclusively by mitosis of a type not very dissimilar from that of *Synchytrium*, but no astral bodies were seen. The chromosomes are approximately six in number. Segmentation is believed to be simultaneous, and begins at least before the sporangium enters the period of rest which it often undergoes before sporulation. The formation of resting spores was found to be dependent on conditions in the culture which are described. The small adjacent cells are definitely shown to be antheridia and the transfer of their coenocytic protoplasm to that of the egg is figured. The number of nuclei of the gametes unfortunately is not stated, but one would judge from the figures that it approximates 100. The fate of the male pronuclei after entering the egg could not be definitely followed, but it is believed that they fuse in pairs with the female pronuclei. The author concludes that "these forms seem to be primitive sexual organisms of the oomycete type. The influence of external conditions on the development of the sexual stage, the mode of fertilization, the unequal size of the two gametes, and the apparent morphological equivalence of these gametes with the sporangia, seem to the writer to point to that assumption."—ROBERT F. GRIGGS.

An epiphytic Tillandsia.—The "ball moss," *Tillandsia recurvata*, is found growing epiphytically upon many tree species in the vicinity of Austin, Texas, in such abundance as to be detrimental to its host. BIRGE[17] has found that any damage resulting to the supporting tree must be due to interferenc with the light supply, as the short holdfast roots merely furnish mechanical support for the moss, the water and salts necessary for the life of the plant being absorbed exclusively by the scale-covered leaves. A sufficient amount may be obtained from three hours dew or rain to last the plant for 38 hours. The leaves are well supplied with chlorophyll in minute oblong plastids, and the complete independence of the plant is shown not only by the entire absence of any organic connection with the living tissues of the host, but also by the fact that it thrives upon old board fences and even upon electric wire insulators. It seems to thrive best in semi-arid conditions. Shade trees may be freed from the epiphyte by scraping off the larger plants before the dissemination of

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[17] BIRGE, WILLIE I., The anatomy and some biological aspects of the "ball moss," *Tillandsia recurvata* L. Univ. Texas Bull. 194. pp. 24. *pls.* 10. 1911.

the seed in January, and by the destruction of the seedlings by spraying with a 10 per cent kerosene emulsion.

The study of the morphology of the reproductive organs shows a single archesporial cell giving rise to a parietal cell, which BILLINGS says does not appear in *T. usneoides*. In four or five days after formation the megaspore mother cell begins the divisions that result in a linear tetrad; an embryo sac of the usual type is produced; double fertilization commonly occurs, and the endosperm develops as free nuclei which eventually line the sac and become separated by walls. The development of the embryo is of the usual *Alisma* or *Sagittaria* type characteristic of most monocotyledons. The dispersal of the seeds is facilitated by long barbed hairs arising from the integument, and later functioning in attaching the seeds to the substratum, upon which they speedily germinate. Under favorable conditions germination frequently occurs within the capsule before the dispersal of the seed.—GEO. D. FULLER.

Permeability.— Heretofore the power of various anilin dyes to stain living plant cells has been tested on algae, water plants, root hairs, or thin sections of organs of land plants, a method introduced by the pioneer work of PFEFFER. KÜSTER[18] conceived that surface cells as used in this method may have different permeability characters from the deeper placed ones, also that cells of land plants may have their permeability characters considerably altered by sectioning. In order to test the ability of anilin dyes to penetrate the deeper lying cells in their natural conditions, KÜSTER used twigs of some size, or at least whole leaves with petioles. The cut ends were placed in aqueous solutions of the dyes, which were carried up the xylem by the transpiration stream, and, after 24 hours sections of the organs were studied for staining of the living cells along the xylem strands. A number of anilin dyes that former workers have pronounced incapable of entering living cells KÜSTER finds by this method to be excellent *intravitum* stains. He distinguishes carefully between true *intravitum* staining and staining due to injured protoplasm. In many cases cells were not injured by many days' treatment with dyes, and dyes abundantly stored in living cells were not reduced in amount by several days' washing in running water.

His results furnish much evidence against OVERTON'S lipoid theory of permeability; and in contrast to the results of RUHLAND on plant cells and HÖBER on animal cells, show, with few exceptions, a general parallelism between high diffusibility (non-colloidality) of the aqueous solution of anilin dyes and their ability to penetrate the living cell.—WILLIAM CROCKER.

Chemical unit-characters in maize.—While all inherited characters are probably referable to chemical relations brought about in the segregations and recombinations of the substance and substances of the germ cells, little atten-

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[18] KÜSTER, ERNST, Über die Aufnahme von Anilinfarben in lebende Pflanzenzellen. Jahrb. Wiss. Bot. **50:** 261–288. 1911.

tion has been given thus far to the invisible chemical composition of zygotes in the generations following a cross. PEARL and BARTLETT[19] have investigated a cross between a yellow dent starchy maize and a white sweet maize, and reach the conclusion that low fat content, low protein content, low ash content, and perhaps also low crude fiber and low percentage of pentosans, are inherited as Mendelian unit-characters independent of the units which determine the externally distinguishable characters of color and starchiness. As the method of arriving at this conclusion was indirect, it was impossible to determine whether these chemical characters are also independent of each other. The low grades of all these characters are dominant over high grades. The authors assume that the absence of the genes for starchiness (*ss*) acts as an inhibitor to these chemical units. It would harmonize better with the presence-and-absence hypothesis to regard the low grades of the various chemical substances here considered as the product of the interaction of the corresponding genes with the gene for starchiness. The authors point out that the result of this investigation should lead to a revision of the usual interpretation of the oft-cited selection experiments of the Illinois Agricultural Experiment Station.—GEO. H. SHULL.

Transition from root to stem.—COMPTON[20] has published a very useful analysis of the theories of the anatomical transition from root to stem. Its text is the recent notable publication by CHAUVEAUD which COMPTON regards as marking "an important advance in the study of seedling anatomy." In these days, when many botanists are trying to orient themselves in the very rapidly developing field of vascular anatomy, such comparative statements are very helpful.—J. M. C.

Embryogeny of Ranunculaceae.—SOUÈGES has undertaken the investigation of the embryo sac and embryo of the Ranunculaceae, and the papers dealing with the Clematideae were noticed in this journal.[21] The four most recent papers in the series[22] continue the consideration of the Anemoneae, and comprise a detailed account of *Myosurus minimus*. It is interesting to have the embryogeny of this form so thoroughly worked out and so well illustrated.—J. M. C.

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[19] PEARL, R., and BARTLETT, J. M., The Mendelian inheritance of certain chemical characters in maize. Zeitschr. Ind. Abst. Vererb. **6:** 1–28. *fig. 1.* 1911.

[20] COMPTON, R. H., Theories of the anatomical transition from root to stem. New Phytol. **11:** 13–25. *fig. 1.* 1912.

[21] BOT. GAZ. **51**:480. 1911.

[22] SOUÈGES, E., Recherches sur l'embryogénie des Renonculacées. Bull. Soc. Bot. France **58:** 542–549, 629–636. 1911; **59:** 23–31, 51–56. 1912.

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THE

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OCTOBER 1912

COMPARATIVE ANATOMY OF DUNE PLANTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 161

ANNA M. STARR

(WITH THIRTY-FIVE FIGURES)

The literature of ecological anatomy is extensive when one considers that the whole subject of ecology is a late arrival in the field of botany. Comparative anatomy, ecologically viewed, is limited enough to justify a brief review. BONNIER (**1**) was a pioneer in experimental work, taking parts of plants growing in intermediate situations in the mountains and transplanting one part to the lowlands and another part to alpine conditions. He found that the plants grown in the two habitats differed in appearance, habit, and structure (**2**). GREVILLIUS (**15**) in an extensive work on the island Öland compared the vegetation of the alvar, a dry, rocky, treeless plain, with that of the fertile regions. CHRYSLER (**7**) compared the anatomy of strand plants at Woods Hole with that of the same species growing on the shores of Lake Michigan. CANNON (**5**) at the Desert Laboratory (Tucson) contributed some experiments on desert plants, keeping some plants under irrigation and letting others of the same species grow without irrigation, his study being a comparison of the conductive tissues. CHERMEZON (**6**) in a recent contribution to the anatomy of littoral vegetation makes some comparison of it with that of continental plants. All agree that the structure of plants varies with change in conditions.

In 1899 COWLES (**8**) published the results of his studies of the sand dunes of Lake Michigan, describing the general features of

the coast, the ecological factors, and the plant associations. It was his intention to enter into an investigation of the anatomical relations of the plants described, but other work prevented. In the fall of 1908 he suggested that I undertake the study, and it has been under his direction that the work has been carried on. I wish to express my grateful thanks to him and to all the members of the Department who helped me with criticism and advice, and also to those who aided me in photographic work and in collecting material. In 1904 C. L. HOLTZMAN, in an unpublished dissertation, described the leaves of six of the species included in my work, and I have had access to his paper.

The dune plants were collected from the Indiana dunes, chiefly from the vicinity of Miller's, Dune Park, and Furnessville. The mesophytic forms came mainly from the flood plains of the Desplaines River at Riverside; some were collected in other mesophytic woods in the same general locality, while a few came from the Mississippi flood plain.

The stems and roots were preserved in formalin and 50 per cent alcohol and cut with a hand microtome. The leaves that made the most successful permanent preparations were killed with corrosive sublimate dissolved in 95 per cent alcohol, used hot. These were easily sectioned in paraffin. I found 8 μ the most satisfactory thickness. Free-hand sections were also made. Safranin and anilin blue were used in staining. The names are those given in the seventh edition of GRAY'S *Manual* and differ therefore at times from those used by COWLES. The drawings were made by the aid of a camera lucida, magnified 470 diameters, and reduced one-half in reproduction.

Ecological factors in the dunes

LIGHT AND HEAT.—There is direct illumination, increased by reflection from the sand. Because of the scanty vegetation and the great exposure, the temperature of the air is higher in summer and lower in winter than in more protected localities. Owing to the high conductivity of sand, the same great divergence between extremes is present in the temperature of the soil.

WIND.—COWLES considers this the most potent factor in determining the character of the dune vegetation. The winds

gather force as they sweep across the lake, and when they reach the shore they gather up sand and carry it along with a force that carves and scars the bark of the trees on the windward side or completely wears it away, as in the case of *Cornus stolonifera*.

SOIL.—The soil is chiefly quartz sand, the particles being relatively large, so that it is extremely porous, which has a great influence on the water and heat relations. As a rule sandy soils are poor in nutrient food materials, nor do they rapidly develop a rich humus because of the rapid oxidation of the organic matter.

WATER.—The surface layer of soil is very dry, as the capillarity of sand is less than that of other soils, evaporation from a sandy surface is rapid, and precipitated water percolates quickly, the water capacity of sand being slight. On the other hand, a sandy soil yields its water to plants more freely than other soils, and below the superficial layer of dry sand there is always a surprising amount of water. FULLER (**13**) has found this to be more than double the wilting coefficient of dune soil.

BIOTIC FACTORS.—The only biotic factors of marked influence in the dunes are those associated with the plants themselves when they are once established, humus and shade. Humus influences the temperature of the soil and increases the water content, the number of soil organisms, toxicity, and aeration. Shade influences the germination of seeds and increases the accumulation of humus and atmospheric humidity, and so decreases evaporation. FULLER (**12**) finds that in the cottonwood dunes the evaporation is 21 cc. per day, while on the pine dunes it is 11 cc., in the oak dunes 10 cc., and in the beech-maple forest 8 cc., a descending scale from the pioneer formation to the climax forest.

Description of the plants

I. XEROPHYTIC FORMS

Herbs

Cakile edentula.—A small, very succulent annual. Leaves smooth and thick; outer walls of epidermis 4 μ; several rows of palisade on each side with a narrow zone of sponge in the center; water-storage tissue about the bundles; stomata on both surfaces; conductive elements not well developed. Stem with epidermal walls thickened all around, the outer 10 μ.

Euphorbia polygonifolia.—A little prostrate succulent annual with abundant latex. Leaves small, thick, inclined to be folded at right angles on the midrib; walls of epidermis thickened, outer 9–12 μ on the upper surface and 15 μ at the edges of the leaf; stomata sunken to the depth of the epidermis; a layer of palisade cells next the upper epidermis and "festoon" palisade about the bundles; a layer of water-storage tissue next the lower epidermis; cells at the bend of the midrib collenchymatous; small development of vascular elements. Stem woody for so small a plant, having a compact vascular cylinder; walls of epidermis thick, outer 8 μ, cuticle 4.6 μ; cells below thickened; latex tubes conspicuous.

Corispermum hyssopifolium.—Low, branching, succulent annual. Leaf thick, narrow, linear; two layers of palisade on both sides and water-storage tissue in the center; walls of the epidermis thickened, outer 16 μ; cells with thickened walls about the midrib at the edges of the leaf. Stem with two layers of palisade in the cortex and collenchyma at the surface; walls of epidermis heavy, outer 9.6 μ. Root sclerenchymatous except a few outer layers.

Artemisia caudata and *A. canadensis*.—Stout, bushy biennials or perennials. Leaf divided, divisions thick, smallest almost cylindrical, generally pubescent; double row of palisade on both surfaces, water-storage tissue inside; walls of epidermis thickened, outer wall 6–11 μ; stomata sunken one-half the depth of the epidermal cells. Stem with pith rapidly reduced after the first year, small in older, a dense cylinder of wood extending almost to the center; great masses of fibers capping the phloem; outer layers of cortex collenchymatous; considerable cork.

Cirsium Pitcheri.—Biennial, tomentose. Leaf very thick, with revolute margins; epidermal cells small, with thickened walls, outer 6.4 μ; chlorophyll confined to 2–4 outer layers of cells; the rest water-storage tissue with cells increasing in size toward the center with large air spaces between. Stem generally hollow, cortex thick, bundles few, with large vessels and masses of heavy fibers; rays wider than the bundles, the cells with thickened walls, outer cells of cortex collenchymatous.

Lathyrus maritimus.—A smooth trailing perennial herb. Leaf with palisade occupying almost half of the mesophyll, the sponge tissue rather compact; fibers above and below the bundles. Stem sharply angled; phloem capped by a heavy crescent of sclerenchyma; a second ring of sclerenchyma penetrating a distance between the bundles; medullary rays thin; outer wall of epidermis 6.2 μ. Root with large vessels; about one-half the pith made up of scattered masses of sclerenchyma.

Ammophila arenaria.—A stout perennial grass with firm creeping rootstocks that anchor the dunes. Leaf with morphologically upper surface rolled in; the surface a series of ridges and grooves; bundles under the ridges; edges of the leaf and ridges strengthened with hypodermal sclerenchyma, that in the ridges extending into the bundles; upper epidermal cells large and globular, or prolonged into conical hairs; stomata on the upper surface sunken to the depth of the epidermal cells; chlorenchyma reduced to strands each side the bundles; air spaces very small; outer wall of the lower epidermis (the exposed side) 6.4 μ thick, the cuticle 3.2 μ. Stem with cortical tissue sclerenchymatous; walls of the epidermis slightly thickened all around.

Andropogon scoparius (bunch-grass).—Leaf stiffened with a series of bundles, large ones alternating with three small ones, the space above the small ones filled in with three or four enormous epidermal cells and smaller, hypodermal, colorless cells; epidermal cells occasionally prolonged into sharp hairs, longer than those of *Ammophila;* the large cells collapse at the bend of the leaf, as it folds with the upper surface in; masses of sclerenchyma above and below the large bundles and below the middle of the small ones; chlorenchyma above the bundles; outer wall 9.3 μ; cuticle, thick; stomata on lower surface not sunken.

Calamovilfa longifolia.—A rigid perennial grass with horizontal rootstocks and pubescent sheaths; another dune former. Leaf with lower surface plane; with ridges and narrow depressions on the upper surface which rolls in as in *Ammophila;* walls of epidermis thick, cuticle thick; bundles in the ridges with sclerenchyma above and below, and sometimes about the phloem; hypodermal sclerenchyma next to the lower surface and at the top of the ridges; short,

pointed hairs on the upper surface; chlorenchyma, a layer of palisade, and a layer of spherical cells about the bundles; walls of parenchyma cells sometimes folded in as in *Pinus;* stomata sunken as in *Ammophila.* Stem with bundles more numerous toward the periphery, where the cells of the fundamental tissue become smaller; epidermal cells very small.

Solidago racemosa Gillmani (fig. 1).—A perennial herb, woody at the base. Leaf with outer wall of lower epidermis 8 μ thick, cuticle 2.4 μ; chlorenchyma above and below; water-storage tissue in the center; chlorenchyma above scarcely palisade-like, but of two or more layers of slightly elongated cells forming a compact tissue; good development of bundles in the midrib. Stem with small pith; cortex thick, containing groups of fibers and occasionally sclereids, outer layers collenchymatous; crystals in the cells of the pith. Root with ground tissue of sclerenchyma; outer cells of cortex collenchymatous.

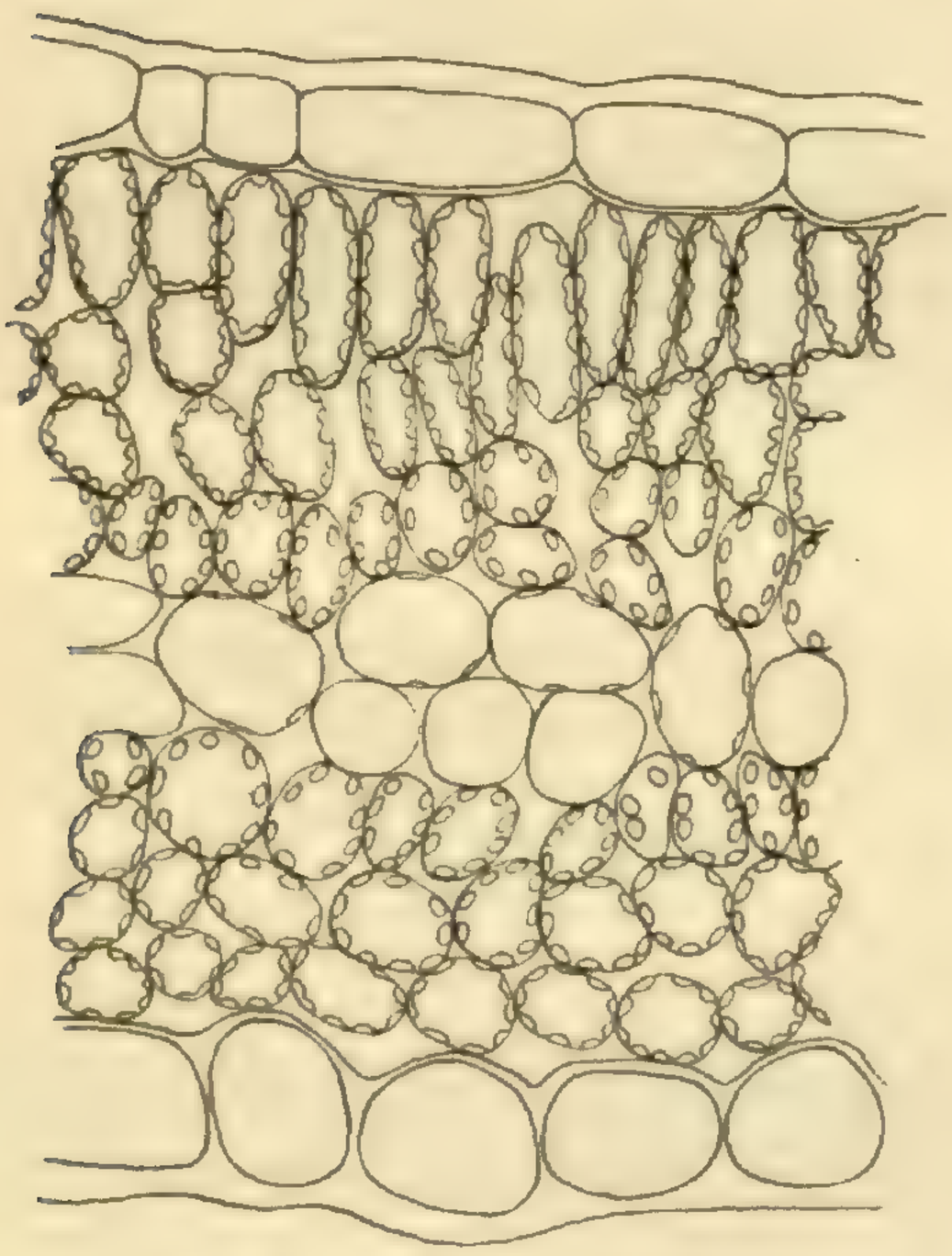


FIG. 1.—*Solidago racemosa Gillmani:* section of leaf.

Lithospermum Gmelini.—A perennial herb clothed with bristly hairs. Leaf thick, coarse, rough on both surfaces, with appressed hairs, bent upward at the midrib; outer wall of epidermis thick on both surfaces, 9.3μ; palisade next both epidermal layers made up of a row of long cells, or of two rows of shorter cells; three layers in the center almost colorless; stomata not sunken. Stem with a small solid cylinder of wood made up chiefly of fibers, the vessels large; outer layers of cortex slightly collenchymatous; outer wall of epidermis 5μ thick.

Arenaria stricta.—A low, tufted herb. Leaf smooth, needle-like; epidermal cells enormous, thickened on all sides especially at the edges of the leaf; outer wall 3.2–7 μ; cuticle thick; sclerenchyma below the bundles; whole mesophyll composed of compact tissue; no palisade; crystals frequent.

Opuntia Rafinesqui.—Stem doing the chlorophyll work; outer wall of epidermis 8 μ thick, cuticle 2.4 μ; several hypodermal layers of small heavy-walled cells; the chlorenchyma composed of many layers of cells elongated perpendicularly to the surface; the center of the stem occupied by a loose tissue of large colorless cells, the whole retaining water so effectually that it is difficult to dry it out even with heat and pressure; vascular system poorly developed; walls of the elements thin.

Shrubs

Prunus pumila.—A low shrub spreading easily in all directions and thus important in helping to make dunes stationary. Leaf thick, 216 μ; outer wall of epidermis 5–6 μ; cuticle very thick, ridged on the lower surface, the ridges so high that they fray out along the edge; cells above and below the midrib papillate and cuticle smooth, 8 μ; heavy masses of collenchyma above the stele of the midrib and several layers below, also in other large veins; great development of conductive elements; palisade double and festoon palisade above the bundles in the veins; lower cells of mesophyll palisade-like; crystals, oil, and other deposits abundant. Stem with vessels large and generally numerous; wood fibers heavy, with small lumen; groups of sclerenchyma in the cortex; cork thick.

Salix syrticola.—A shrub with the same habits as *Prunus pumila.* Leaf with upper surface silky, lower hairy, closely serrate, glandular; stipules large; outer wall of upper epidermis thick; heavy sclerenchyma above and below the stele of the midrib, and collenchyma next the epidermis on both sides; two layers of palisade next the upper epidermis and three more layers elongated vertically. Stem with medullary rays very narrow; vessels not large but numerous; fibers heavy, with small lumen; outer layer of pith sclerenchymatous; outer layers of cortex collenchymatous; three rows of mechanical fibers in the cortex, the outermost very wide.

Hudsonia tomentosa.—A bushy, heathlike shrub. Leaf small, awl-shaped, hairy on both surfaces and especially along the edges; upper epidermis composed of large cells; palisade about one-half the mesophyll of the narrow part of the leaf. Stem hairy, very woody, the vascular cylinder occupying most of the diameter, composed of very heavy fibers and few vessels; a few large scleren-

chymatous cells form the pith; a few rows of cells, part of them fibrous, form the cortex.

Arctostaphylos Uva-ursi.—A woody little plant trailing over the ground. Leaf thick, smooth, evergreen; outer wall of epidermis of both surfaces thick, cutinized; side walls plane, cutin sometimes 16 μ thick; upper epidermis sometimes divided periclinally; bundles compactly developed, with fibers above and below; collenchyma next the epidermis; palisade several rows of shorter cells or two rows of longer; all mesophyll cells elongated perpendicularly to the surface; stomata sunken one-half the depth of the epidermal cells. Stem with xylem cylinder very woody; walls of pith and medullary ray cells heavy; cortex and phloem zones very narrow; cork layer not strikingly thick but very dense; 9 years' growth in a stem 4 mm. in diameter.

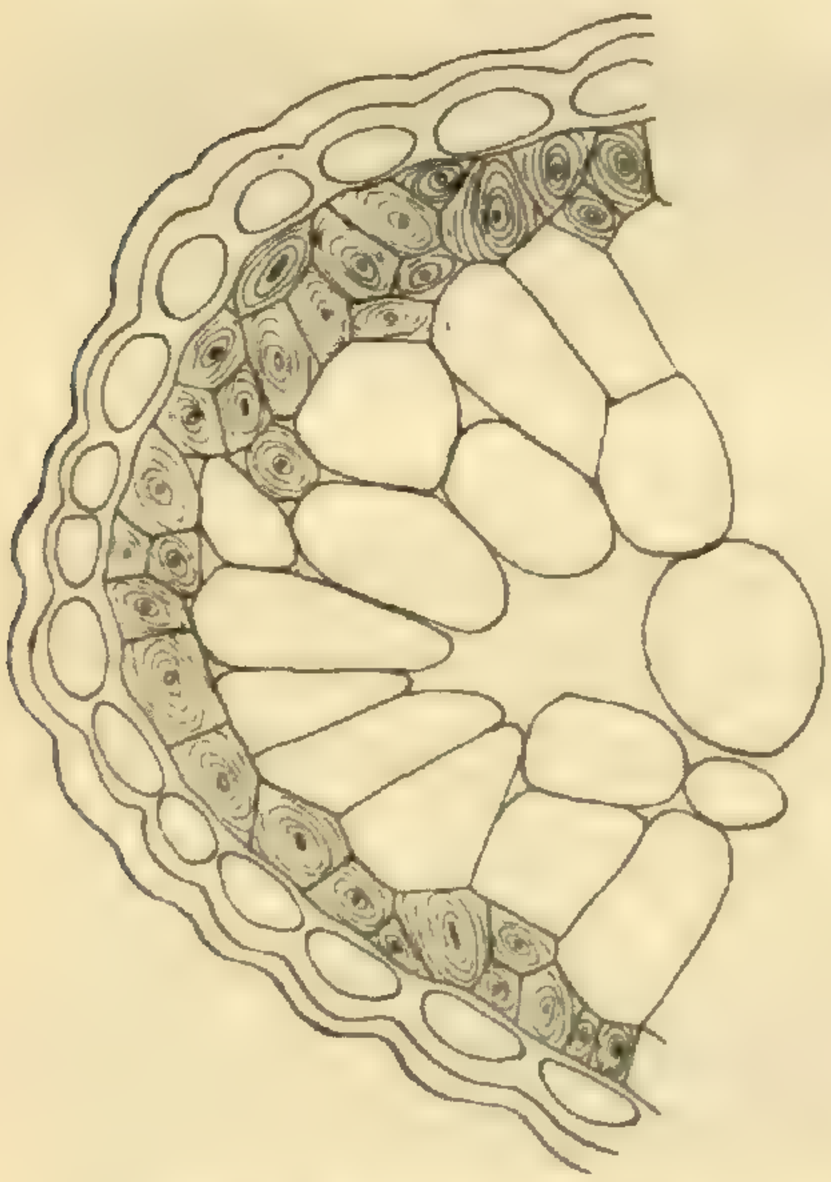


FIG. 2.—*Juniperus communis:* section of leaf.

Juniperus communis (fig. 2).—An erect evergreen shrub. Leaf thick, rigid, convex on one side, concave on the other which is the morphological upper side and is most protected when the leaves are appressed to the stem; stomata on this side at the base of the epidermal cells, guard cells with thickened walls; outer and side walls of epidermis thick, outer 11–13 μ with cuticle 3.2 μ; hypodermis heavy; resin duct on convex side. Stem with almost no pith and heavy wood cylinder; 13 years' stem 4 mm. in diameter; cork thick.

Juniperus virginiana.—A shrub or small tree. Leaf awl-shaped; outer wall of epidermis very heavy, 9.6 μ, cuticle 4.8 μ; two or three hypodermal layers on the convex side of the leaf heavily thickened; sunken stomata on upper plane surface, the protected side when the leaf is appressed. Stem with solid mass of heavy-walled tracheids and almost no pith; 11 growth rings in a stem 4.5 mm. in diameter; rows of sclereids in the cortex; cork thick.

Hypericum Kalmianum (fig. 3).—A bushy shrub. Leaf revolute, thick, leathery; outer wall of epidermis 4.8 μ, cuticle 2.4 μ, lower epidermal cells inclined to be papillate; double palisade; stomata sunken the depth of the epidermis. Stem with vessels large, fibers heavy, lumen small; pith small, cork thick; three growth rings in a stem 3 mm. in diameter.

Trees

Pinus Banksiana.—Leaf shorter and thicker than in most pines; walls of epidermis heavy; outer 8 μ, cuticle 1.8 μ; hypodermis also heavy; thickness of both increased at the edges of the leaf; outer wall of endodermis thickened and lignified; mesophyll cells with infoldings in the walls; stomata deeply sunken, with an outer and inner vestibule and with walls 3.2 μ thick; two resin ducts. Stem with small pith; woody cylinder large, composed of a solid mass of tracheids with very thick walls.

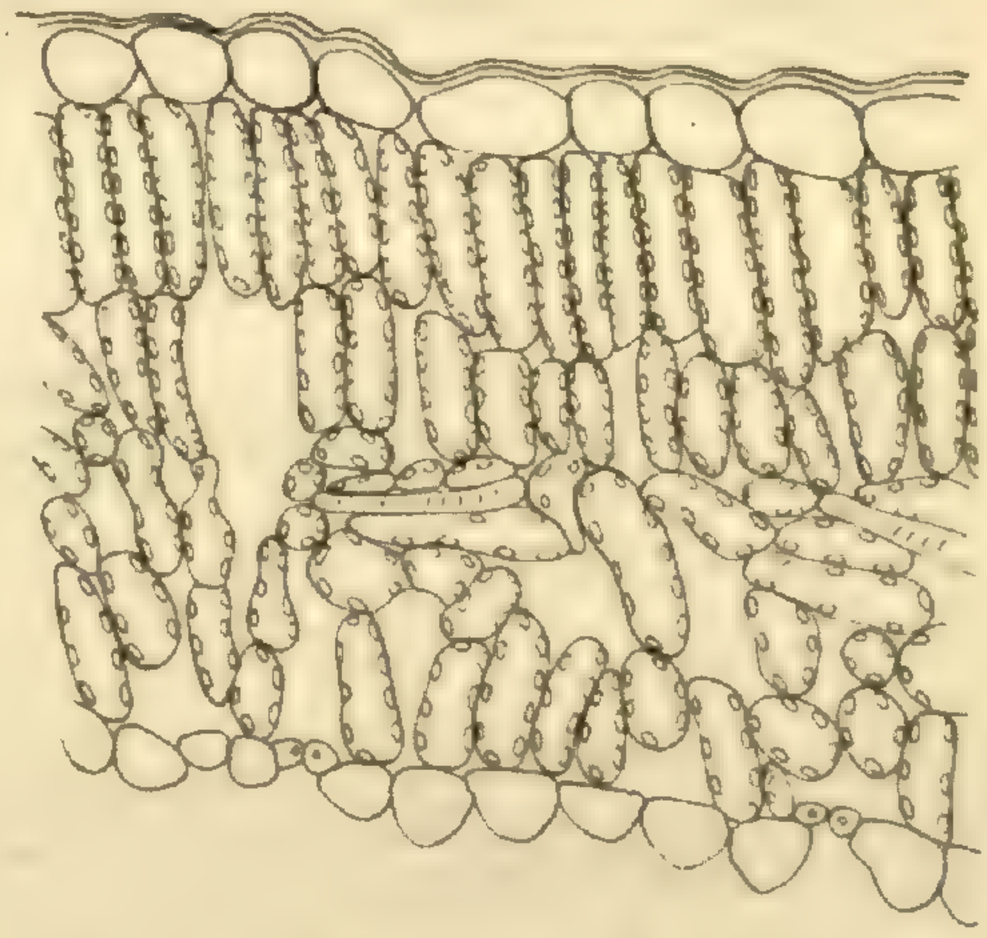


FIG. 3.—*Hypericum Kalmianum:* section of leaf.

Quercus velutina.—Small in comparison with many oaks, and of rather scrubby growth. Leaf thick, having a brilliantly varnished surface; sclerenchyma around the bundles of the midrib; cells above and below collenchymatous; epidermal cells over midrib papillate; outer wall of upper and lower epidermis thickened, cuticle thick; palisade double. Stem with pith star-shaped; vessels large; fibers heavy, with small lumen; medullary rays narrow, pith sclerenchymatous; an irregular band of fibers in the cortex.

Summary of xerophytic characters

The true dune plants have the following characteristics, which, with the exception of the characters of the conductive system, are generally admitted to be xerophytic:

HABIT.—Low, tufted, or bushy, with short internodes (*Arenaria, Artemisia, Hudsonia, Juniperus communis, J. virginiana*); low

and spreading (*Prunus pumila*, *Salix syrticola*); low and trailing (*Lathyrus*, *Arctostaphylos*); low, with underground, creeping rootstocks (*Ammophila*, *Calamovilfa*).

LEAF.—Small and awl-shaped (*Arenaria*, *Hudsonia*, *Juniperus communis*, *J. virginiana*); longer, sometimes wide but thick (*Artemisia*, *Ammophila*, *Calamovilfa*, *Lithospermum*, *Prunus*, *Arctostaphylos*, *Pinus*, *Hypericum*, *Cakile*, *Quercus*, *Corispermum*); evergreen (*Arctostaphylos*, *Juniperus communis*, *J. virginiana*, *Pinus*); folded or revolute (*Cirsium*, *Ammophila*, *Calamovilfa*, *Lithospermum*, *Hypericum*, *Euphorbia polygonifolia*); succulent (*Cakile*, *Euphorbia polygonifolia*, *Corispermum*, slight in *Artemisia*, *Cirsium*, *Solidago*); hairy (*Artemisia*, *Cirsium*, *Lithospermum*, *Salix syrticola*, *Hudsonia*); equilateral (*Cakile*, *Corispermum*, *Artemisia*, *Cirsium*, *Lithospermum*).

ANATOMY OF LEAF.—Outer wall of epidermis thick (*Cakile*, *Euphorbia polygonifolia*, *Corispermum*, *Artemisia*, *Cirsium*, *Ammophila*, *Calamovilfa*, *Andropogon*, *Solidago*, *Lithospermum*, *Arenaria*, *Prunus pumila*, *Salix syrticola*, *Arctostaphylos*, *Juniperus communis*, *J. virginiana*, *Pinus Banksiana*, *Hypericum*, *Quercus velutina*, *Opuntia*); cuticle thick (*Ammophila*, *Calamovilfa*, *Andropogon*, *Solidago*, *Arenaria*, *Prunus pumila*, *Arctostaphylos*, *Juniperus communis*, *J. virginiana*, *Pinus Banksiana*, *Hypericum*, *Quercus*, *Opuntia*); deep, compact palisade accompanied by few air spaces in sponge (*Artemisia*, *Lathyrus*, *Lithospermum*, *Prunus pumila*, *Salix syrticola*, *Hudsonia*, *Arctostaphylos*, *Hypericum*, *Quercus velutina*, *Cakile*, *Corispermum*); stomata sunken (*Artemisia*, *Ammophila*, *Calamovilfa*, *Hypericum*, *Euphorbia polygonifolia*, *Arctostaphylos*, *Juniperus communis*, *J. virginiana*, *Pinus*); conductive tissue well developed (*Solidago*, *Prunus*, *Arctostaphylos*); mechanical tissue present as sclerenchyma (*Lathyrus*, *Ammophila*, *Calamovilfa*, *Andropogon*, *Salix syrticola*, *Arctostaphylos*, *Quercus*), as collenchyma (*Solidago*, *Andropogon*, *Prunus*, *Salix syrticola*, *Arctostaphylos*, *Quercus*, *Euphorbia polygonifolia*).

ANATOMY OF STEM.—Succulent (*Opuntia*); conductive tissue well developed, with vessels large (*Cirsium*, *Lithospermum*, *Prunus*, *Hypericum*, *Quercus*), with vessels numerous (*Salix syrticola*, *Prunus pumila*); mechanical tissue present, an abundance of wood

fibers giving general "woodiness" (*Euphorbia polygonifolia, Artemisia, Cirsium, Lithospermum, Prunus, Salix syrticola, Hudsonia, Arctostaphylos, Pinus, Hypericum, Juniperus communis, J. virginiana, Quercus*), as sclerenchyma (*Artemisia, Lathyrus, Ammophila, Solidago, Prunus pumila, Salix syrticola, Hudsonia, Quercus, Juniperus virginiana*), as collenchyma (*Artemisia, Cirsium, Solidago, Lithospermum, Salix syrticola, Pinus, Corispermum*); outer wall of epidermis thick (*Cakile, Euphorbia, Lathyrus, Ammophila, Lithospermum*); cork thick (*Artemisia, Prunus, Hypericum, Juniperus communis, J. virginiana*).

ANATOMY OF ROOT.—Sclerenchymatous generally (*Cakile, Corispermum, Lathyrus, Solidago*); collenchyma in cortex (*Solidago*); crystals abundant (*Solidago, Arenaria, Prunus*); resin (*Juniperus communis, J. virginiana, Pinus*); latex (*Euphorbia*); perhaps none but the last is related to xerophytic conditions.

Slowness of growth is shown by the large number of growth rings in stems of small size (*Arctostaphylos, Hypericum, Juniperus communis, J. virginiana*), testifying to adverse conditions. Succulency usually excludes some other factors, as hairiness and good development of conductive elements.

FITTING (**11**) has recently shown that desert plants apparently do not need longer roots to reach an abundant water supply, as they have a most effective means of obtaining it from a very scanty supply in the high osmotic pressure of their cell sap. Dune plants have not been examined in this respect. It may be found that they too have this "adaptation" to xerophytic conditions.

II. COMPARISON OF PLANTS GROWING ON THE DUNES WITH THE SAME SPECIES GROWING IN MESOPHYTIC SITUATIONS

The purpose of this part of the investigation was to find out by careful measurements just how much variation there is in species found in two widely differing habitats. The measurements of sections were made with a micrometer divided into 100 spaces. For the measurement of the leaf, sections were made near the middle, cutting straight across the midrib; an average was taken of several measurements of one leaf and then of several leaves. For

the study of the conducting and mechanical tissues of the leaf, a section of the midrib was taken at the base of the blade. For the study of the stems, sections 5 mm. in diameter were used; when this was not possible, the two compared were as nearly equal as obtainable. CANNON'S method of counting was adopted. A circle 14 cm. in diameter was drawn on paper and octants were marked off. With a camera lucida an image of the section was so thrown on the paper that the arc of the octant coincided as nearly as possible with the periphery of the wood cylinder. The area of the octant was 18.24 sq. cm. ($14^2 \times 0.7845 \div 8$). Since the magnification used was 100, the area examined was 0.19 sq. cm. or 19 sq. mm. For the size of the vessels and fibers measurements were always made in the last spring wood, or if that was not fully organized, in the preceding. In the following tables *M* stands for the mesophytic form and *X* for the dune form; *T* for the average thickness of leaf, with minimum and maximum in parenthesis; *UE* for thickness of the upper epidermis, including cuticle; *P* for depth of palisade; *Sp* for depth of sponge; *LE* for thickness of lower epidermis; *OW* for outer wall of the epidermis (including cuticle); and *Cu* for cuticle. The percentages are of the entire thickness of the leaf. In the table of stems *N* stands for the number of vessels in the octant; *D* for the average diameter of the larger vessels, with the maximum in parenthesis; *W*, the thickness of the walls of the vessels; *F*, the thickness of the walls of the fibers; *L*, the lumen of the fibers; *R*, the number of growth rings; *C*, the thickness of cork; and *S*, the thickness of the sclerenchyma ring or of the isolated masses of sclerenchyma that often appear in the cortex. As the size of vessels, being tubes, varies as their cross-sections and as the cross-sections vary as the squares of their radii, it is evident that the vessels in an octant of a mesophytic form would compare with the vessels in an octant of the corresponding dune form as the products of the number of vessels by the squares of their radii. Where the result is not evident at a glance, the radius was squared and the product found. The measurements are all in microns, though the μ is omitted after the first, as is also the per cent sign.

Trees

ACER SACCHARUM

	Leaf		Stem	
	M	*X*	*M*	*X*
T.....	75 μ (69–93)	103 μ (95–109)	N... 41	33
UE...	10.5 =14 per cent	13 =12 per cent	D... 36 μ (50)	37 μ (46)
P.....	29.5 =39	40 =39	W... 3	3.5
Sp....	29.0 =39	40 =39	F.... 4.2	4.7
LE...	6.0 = 8	10 =10	L.... 6.2	8.5
OW...	1.6	3.5	R... 3–5	2–4
Cu...	thin	1.7	C.... 80	72
			S.... 64	50

X.—Hairs on lower surface; upper epidermal cells smaller in depth, slightly larger in surface extent; outer wall and cuticle thicker; sclerenchyma around the bundles of the midrib heavier; greater development of bundles; cuticle on upper surface more strongly ridged. In both stomata on lower surface only.

In all points but the thickness of the walls of the vessels and the fibers, an exception to the majority of cases examined.

CELTIS OCCIDENTALIS

	Leaf		Stem	
	M	*X*	*M*	*X*
T.....	65 μ (87–72)	120 μ (104–144)	N... 17	18.5
UE...	13 =20 per cent	24 =20 per cent	D... 74 μ (101)	74 μ (120)
P.....	14 =22	43 =36	W... 2.4	3.2
Sp....	24 =37	40 =33	F.... 4.8	6.4
LE...	14 =21	13 =11	L.... 4.8	3.2
OW...	0.7	3	R... 7	7
Cu...	very thin	0.7	C.... 48	32
			S.... 64	80

X.—Large glandular cells frequently occupying the place of the epidermis and palisade; collenchyma below and sclerenchyma above the midrib, where neither appears in the mesophytic form; greater development of vascular elements.—Figs. 4 and 5.

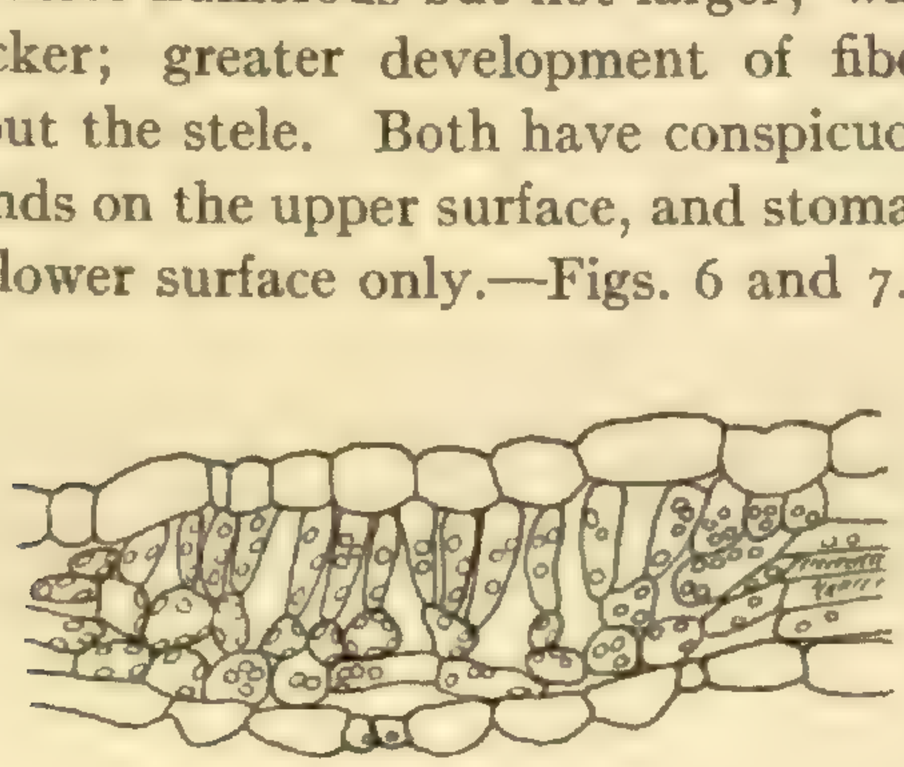
X.—A straggling shrub, probably var. *pumila;* slightly greater development of vessels with heavier walls; fibers heavier, but fewer of them than in *M*, replaced by tracheids; cork thinner; more sclerenchyma in the cortex.

FRAXINUS AMERICANA

	Leaf		Stem	
	M	*X*	*M*	*X*
T.....	142 μ (124–159)	162 μ (142–187)	N... 22.5	19.5
UE...	11 = 8 per cent	14 = 9 per cent	D... 53 μ (87)	51 μ (72)
P.....	52 =36	68 =42	W... 3.7	3.9
Sp....	68 =48	59 =36	F.... 3.2	4.5
LE...	11 = 8	21 =13	L.... 7.2	7.3
OW...	1.5	3	R... 88	110
Cu...	0.7	1.8	C.... 53	99
			S.... 3–5	1–2

X.—Epidermal cells of greater depth; outer wall and cuticle thicker, ridged in the lower epidermis, most of the cells of the lower epidermis produced into short conical hairs, the rest into long hairs (*M* smooth); all tissue more compact; palisade deeper, tending to develop four rows (*M* only two); vessels in the mid-rib more numerous but not larger; walls thicker; greater development of fibers about the stele. Both have conspicuous glands on the upper surface, and stomata on lower surface only.—Figs. 6 and 7.

X.—Differing from the majority in number and size of vessels and more rapid growth; walls of vessels and fibers thicker; sclerenchyma and cork heavier. In both walls of pith-cells thickened with conspicuous canals, and outer cortex collenchymatous, features pronounced in *X*.



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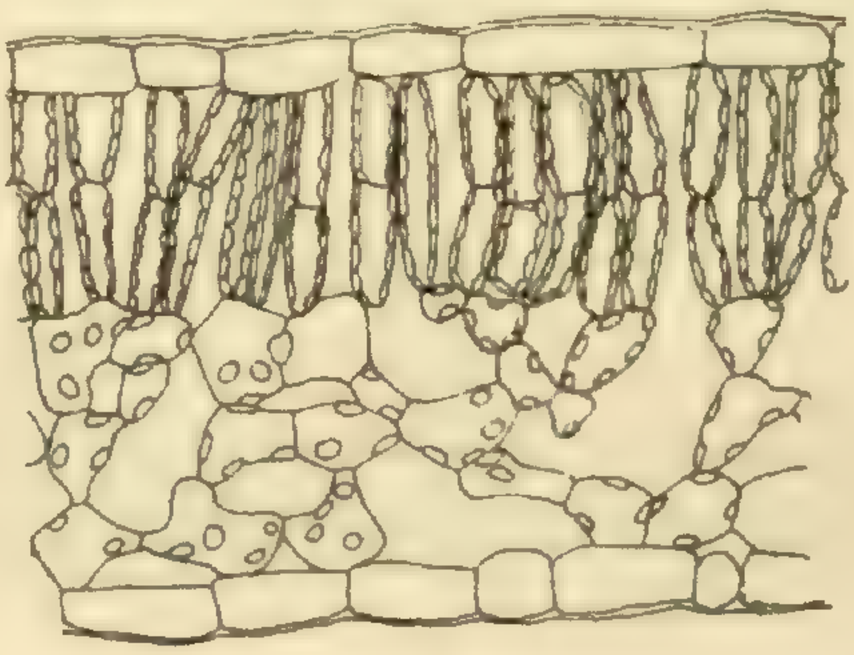

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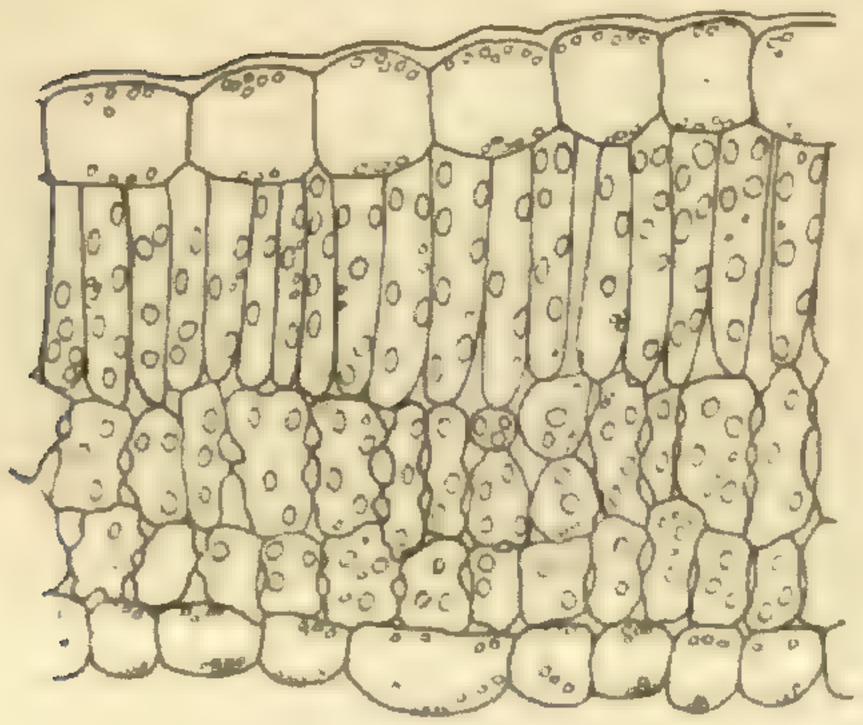

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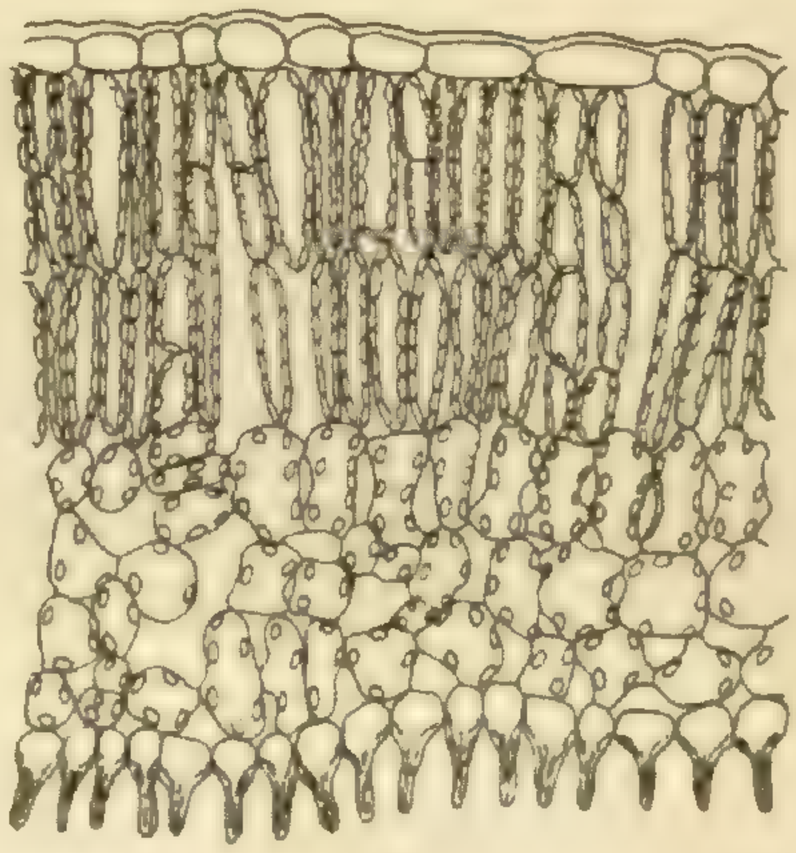

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FIGS. 4–7.—Figs. 4 and 5, *Celtis occidentalis:* sections of leaves; fig. 4, mesophytic form; fig. 5, dune form; figs. 6 and 7, *Fraxinus americana:* sections of leaves; fig. 6, mesophytic form; fig. 7, dune form.

JUGLANS CINEREA

	Leaf		Stem	
	M	*X*	*M*	*X*
T.....	92 μ (79–112)	148 μ (119–166)		
UE...	12 =13 per cent	13 = 9 per cent	N... 18	25
P.....	21 =21	39 =26	D... 64 μ (85)	55 μ (79)
Sp....	44 =48	82 =55	W... 7.3	3.8
LE...	14 =16	14 =10	F.... 4	3.2
OW...	thin	3.7	L.... 9.5	9
			R... 1–6 (av. 3)	1–3
			C.... 60	57
			S.... 73	77

X.—More pubescent; upper epidermal cells smaller in depth, same in surface extent; first layer of palisade deeper and a second layer developed; vessels in midrib of the same size but more numerous; more sclerenchyma and collenchyma; crystals abundant.—Figs. 8 and 9.

X.—Like the majority in the greater number of vessels of smaller area (but the final product greater), the smaller lumen of the fibers, and the heavier sclerenchyma; differing in thinner walls and cork, and occasionally large number of rings produced in *M*

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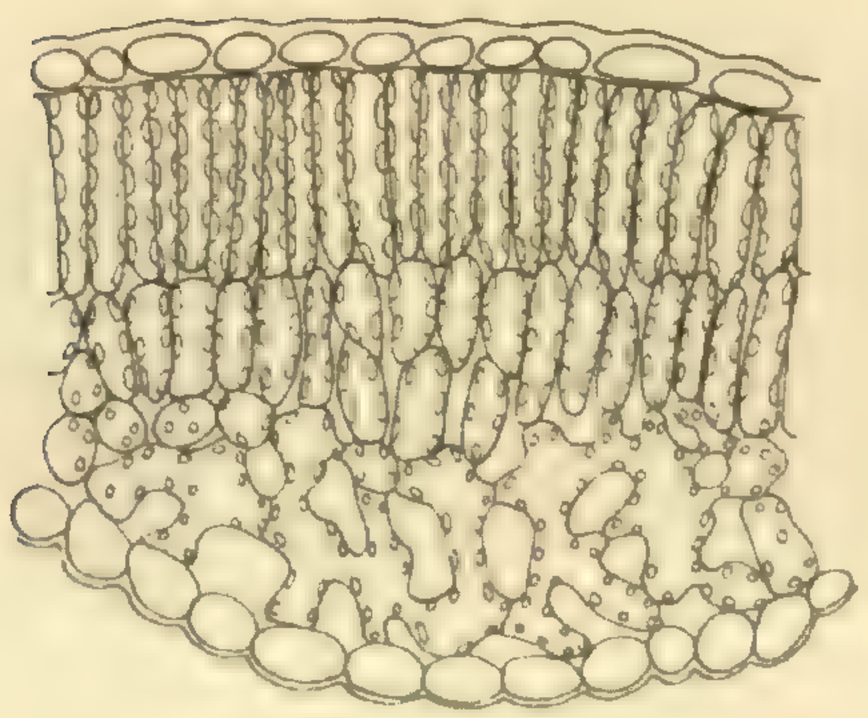

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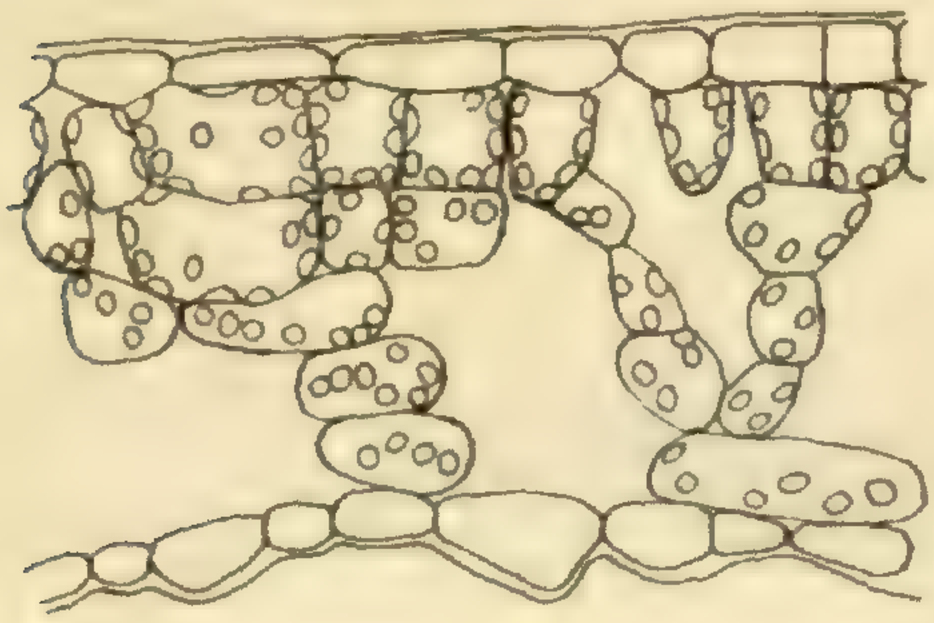
FIGS. 8, 9.—*Juglans cinerea:* sections of leaves; fig. 8, mesophytic form; fig. 9, dune form.

LIRIODENDRON

Leaf			Stem		
	M	*X*		*M*	*X*
T.....	148 μ (137–168)	210 μ (190–236)	N...	79	131
UE...	15 = 10 per cent	17 = 8 per cent	D...	34 μ (48)	32 μ (41)
P.....	37 = 25	59 = 28	W...	3.1	3.2
Sp....	80 = 54	111 = 53	F....	3.8	4.6
LE...	16 = 11	22 = 11	L....	10.7	8.5
OW...	3.3	5.6	R...	1–3	2–5
Cu		2	C....	42	50
			S		

X.—Cells of upper epidermis smaller in surface and depth, side walls plane (wavy in *M*); palisade deeper, sometimes of more layers; cells of upper layer each side of midrib larger than others and without chloroplasts, as if a secondary epidermis; vessels more numerous in midrib; greater masses of fibers and more collenchyma. In both, lower epidermis heavy.—Figs. 10 and 11.

Like the majority in all respects. In both, sclerenchyma around the pith and groups of fibers capping the phloem.—Figs. 12 and 13.



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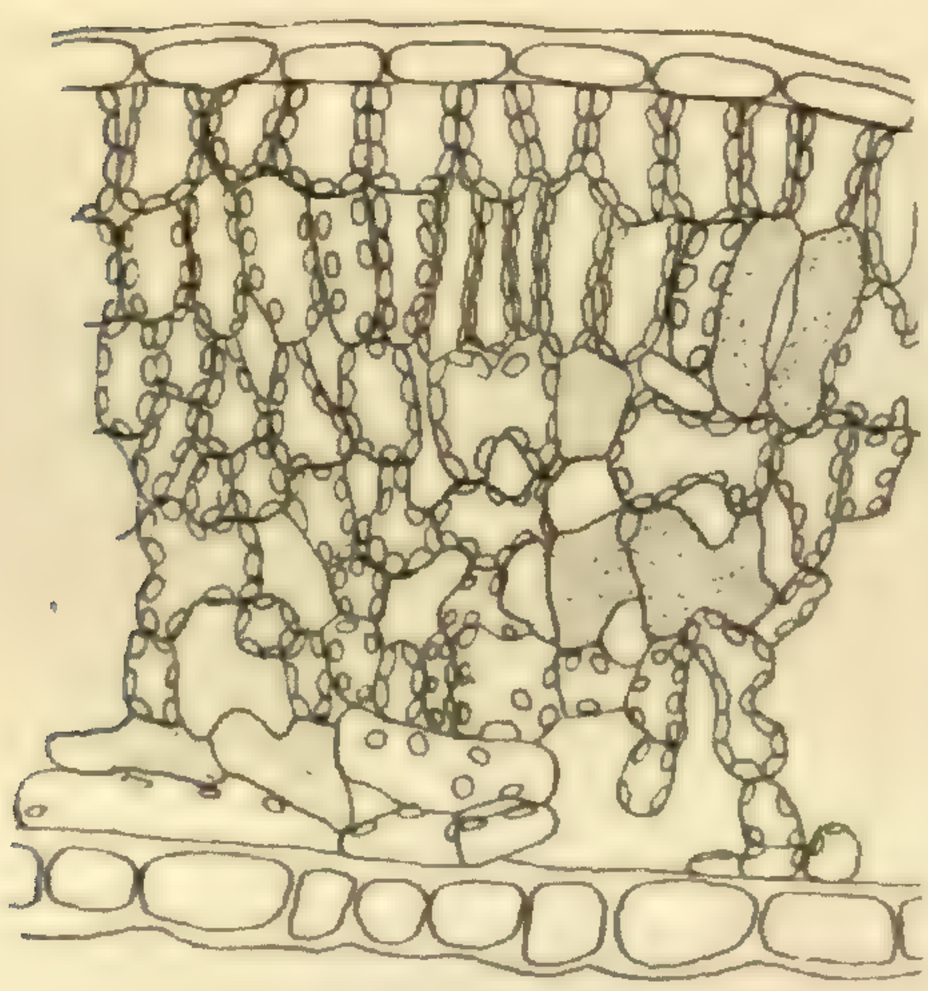

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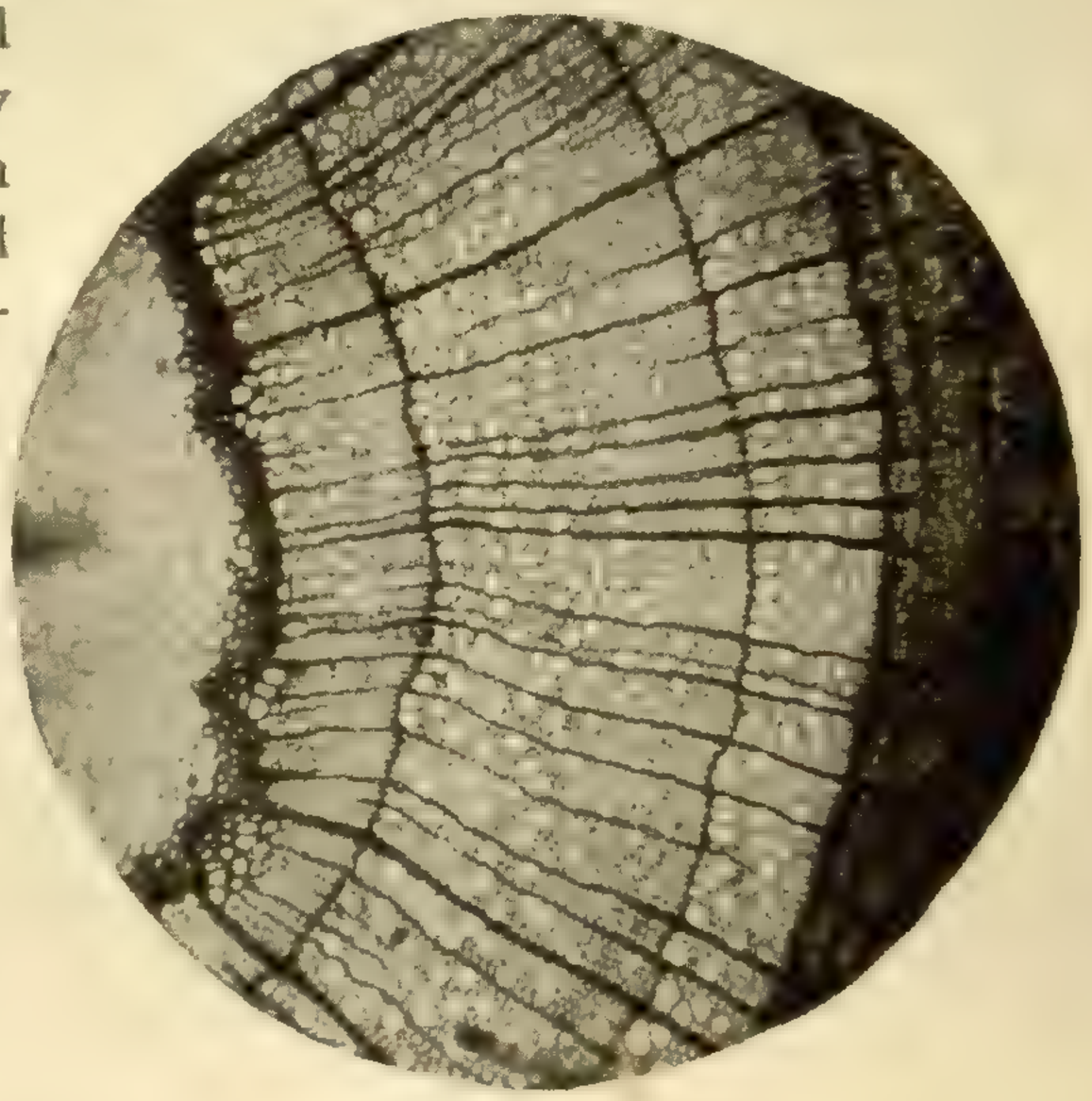

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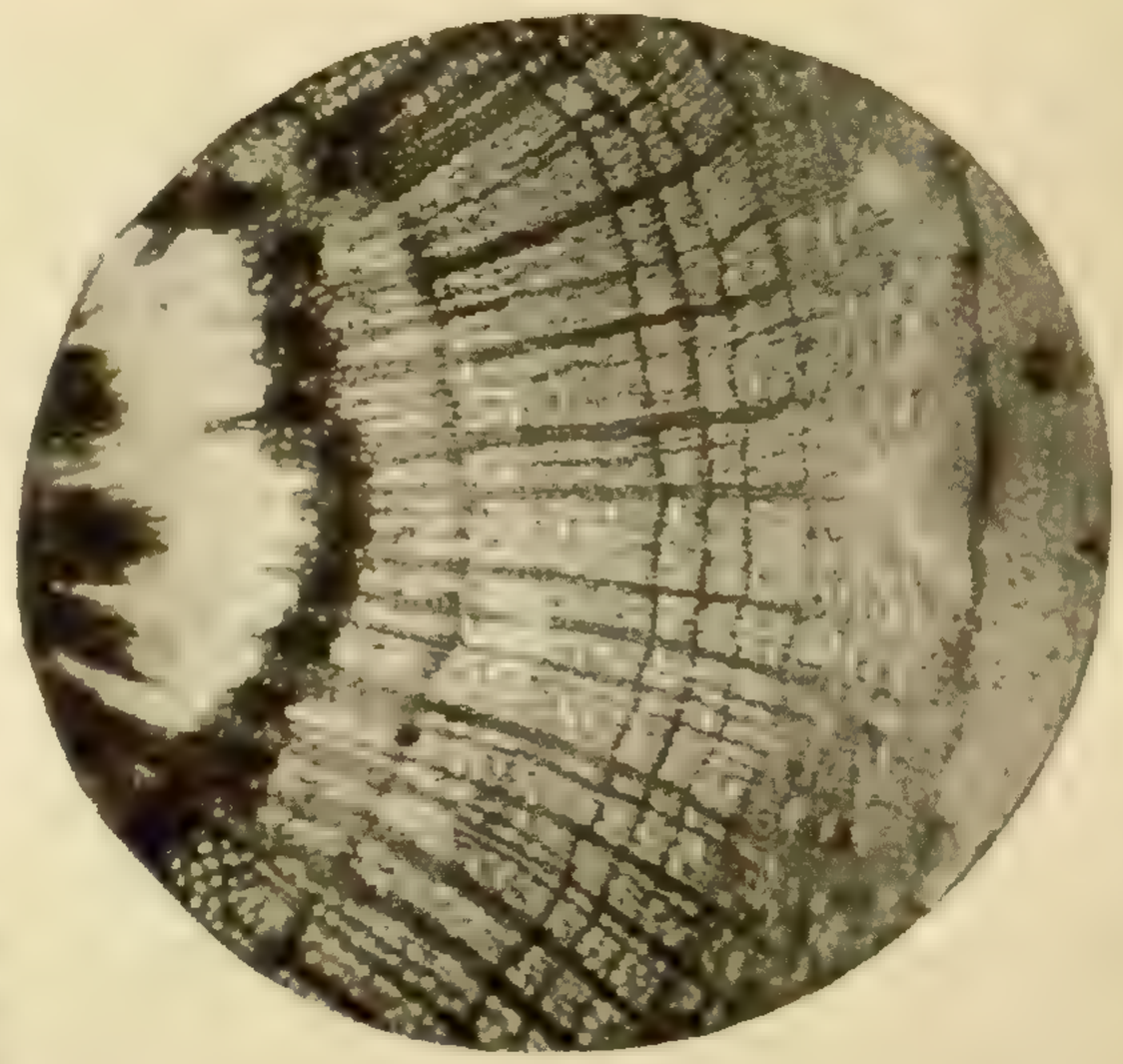


13

FIGS. 10–13.—*Liriodendron tulipifera:* sections of leaves; fig. 10, mesophytic form; fig. 11, dune form; sections of stems; fig. 12, mesophytic form; fig. 13, dune form.

OSTRYA VIRGINIANA

	Leaf		Stem	
	M	*X*	*M*	*X*
T.....	78 μ (66–95)	110 μ (91–125)		
UE...	10 =11 per cent	11 =10 per cent		
P.....	30 =38	43 =39		
Sp....	32	45		
LE...	6	11		
OW...	1.3	3.2		
N...			24	59
D...			48 μ (75)	26 μ (37)
W...			2.8	2.5
F....			3.3	3.9
L....			6.7	5.6
R...			3	3–6
C....			29	64

X.—Upper epidermis slightly thicker and wall thicker; little variation in the depth of the palisade, but the layer more compact; stomata on lower surface only (in *M* occasionally on the upper).

X.—Rings of sclerenchyma in the cortex wider and outer layers of the pith more sclerenchymatous; in all respects, except as to the thickness of the wall of the vessels, agreeing with the majority.

POPULUS BALSAMIFERA

	Leaf		Stem	
	M	*X*	*M*	*X*
T.....	257 μ (243–272)	212 μ (195–228)		
UE...	18 = 7 per cent	17 = 8 per cent		
P.....	96 =37	94 =44		
Sp....	129	89		
LE...	14	16		
OW...	4.3	5		
Cu...	1	1.2		
N			33	90
D...			46 μ (62)	36 μ (50)
W...			2.9	2.6
F....			4.1	3.8
L....			7.2	6.8
R...			1–2	2–9
C....				100
S....			64	90

The only exception found to the general fact that dune plants have thicker leaves than mesophytic. *X*.—Upper epidermis and palisade relatively deeper; outer wall and cuticle thicker and ridged; more vessels in the midrib, larger; more fibers about the stele. Both have stomata on both surfaces; all side walls of epidermis plane except those of lower surface in *M;* double palisade.

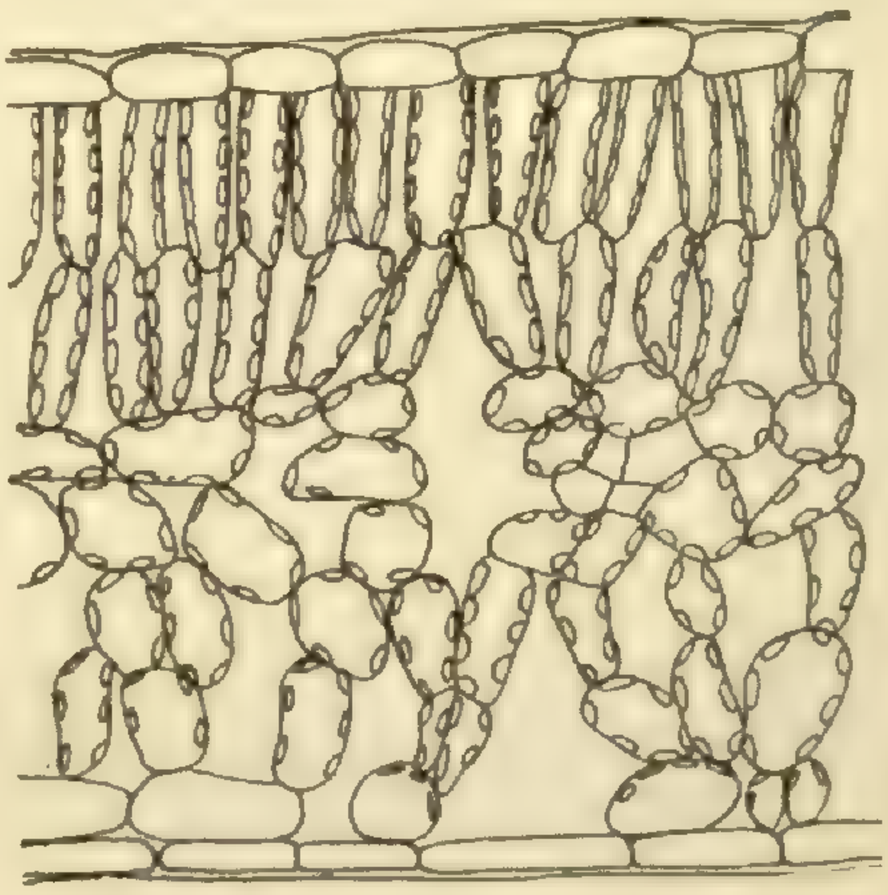
X.—Vessels agreeing with the majority in total area, but walls slightly thinner, walls of fibers also thinner, but lumen smaller, so the amount of wood may be the same; cork only starting to form in *M*.

POPULUS DELTOIDES

	Leaf		Stem	
	M	*X*	*M*	*X*
T.	193 μ (177–227)	254 μ (236–295)	N. . . 46	85
UE. . .	13 = 7 per cent	18 = 7 per cent	D. . . 49 μ (64)	50 μ (62)
P.	62 =32	84 =33	W. . . 2.6	2.7
Sp. . . .	105 =54	138 =55	F. . . . 3.8	3.9
LE. . . .	13	14 = 5	L. . . . 6.8	6
OW. . .	2.3	4	R. . . 2	1–4
Cu. . .	0.8	1.3	C. . . . 82	105
			S. . . . 94	98

In both lower epidermis thickened as well as upper, stomata on both surfaces and side walls of epidermal cells plane, all related to the movement of the leaf. *X*.—Upper epidermal cells smaller in surface; surface slightly hairy; palisade sometimes triple; also palisade cells near lower epidermis, separated from it by a layer of heavily walled cells, like a secondary epidermis. Other points follow the general rule.—Figs. 14 and 15.

Agreeing with the majority in all points; a tendency to angled twigs and star-shaped pith more marked in *X*.



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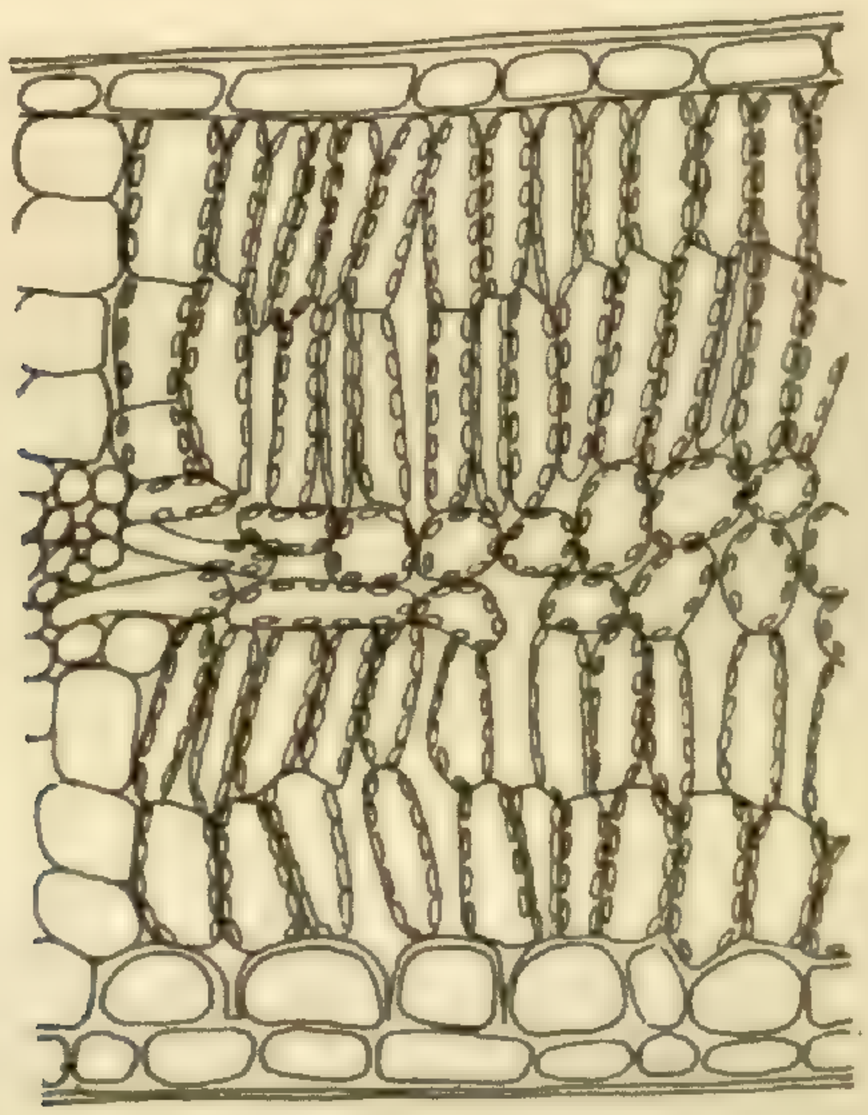

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FIGS. 14, 15.—*Populus deltoides:* sections of leaves; fig. 14, mesophytic form; fig. 15, dune form.

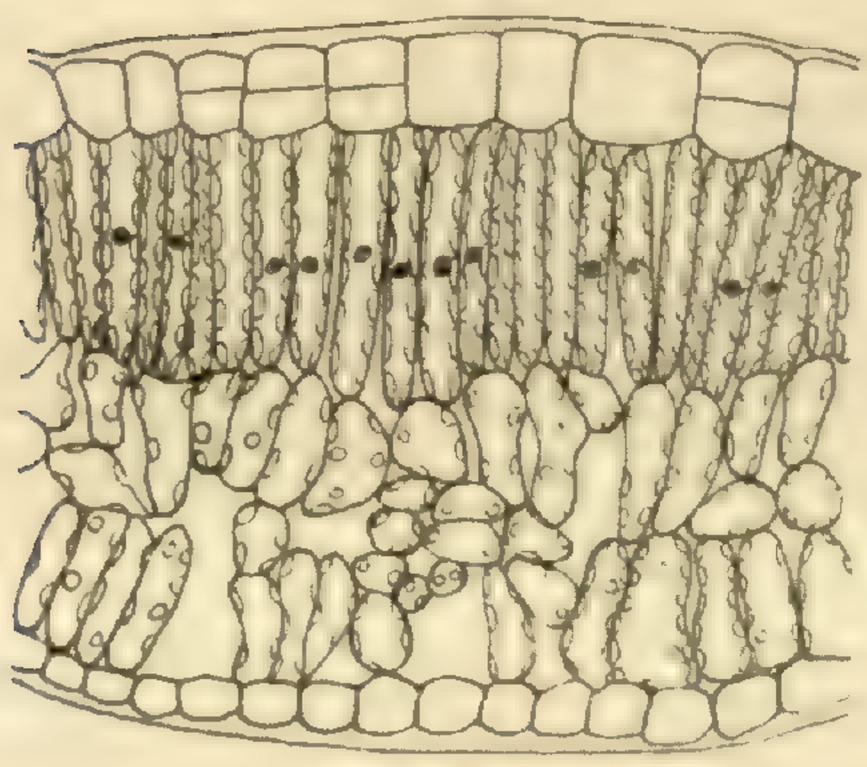
TILIA AMERICANA

	Leaf		Stem	
	M	*X*	*M*	*X*
T.....	90 μ (90–108)	138 μ (135–156)		
UE...	17 =19 per cent	23 =17 per cent	N... 59	63
P.....	26 =29	45 =33	D... 38 μ (53)	41 μ (41)
Sp....	36 =46	52 =38	W... 2.7	2.8
LE...	11 =12	17 =12	F.... 2.8	2.4
OW...	3.7	4.4	L.... 9.6	9.1
Cu...	1.5	2	R... 2–5	1–5
			C.... 58	50

X.—Cells of upper epidermis smaller in depth, larger in surface, sometimes divided periclinally; side walls on lower surface wavy, upper and both in *M* plane; deeper palisade and tendency toward second layer; midrib as in preceding *X*. In both hairs in the axils of the veins; cuticle ridged.—Figs. 16 and 17.

In both bands of sclerenchyma in the phloem and collenchyma under the cork, slightly less in *X;* little variation in walls and lumina of the fibers, but vessels more numerous and larger in *X*.

16



17

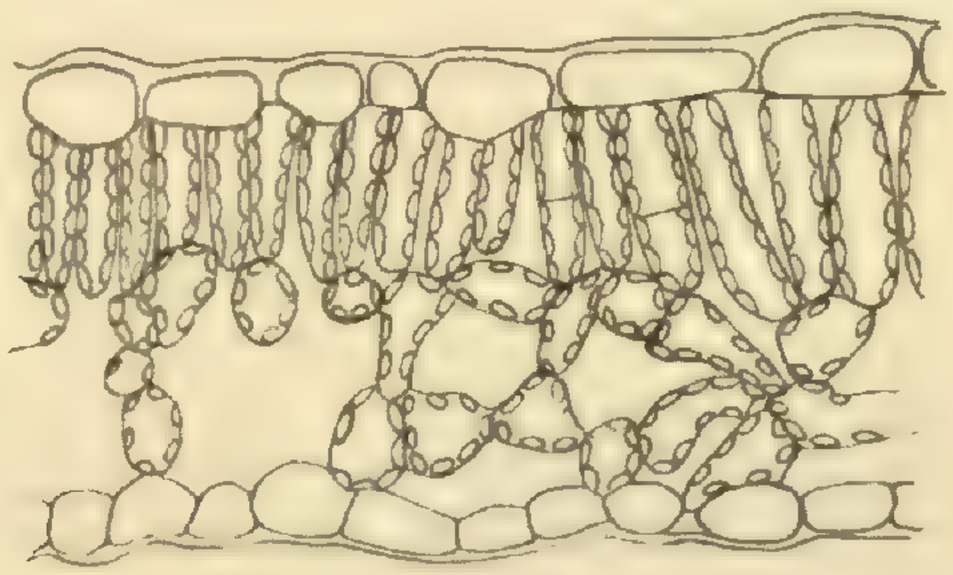
FIGS. 16 and 17.—*Tilia americana:* sections of leaves; fig. 16, mesophytic form; fig. 17, dune form.

ULMUS AMERICANA

	Leaf		Stem	
	M	*X*	*M*	*X*
T.	102 μ (94–109)	174 μ (164–186)	N. . . 28.5	52
UE. . . 21	=21 per cent	38 =22 per cent	D. . . 61 μ (104)	61 μ (96)
P. 29	=29	70 =40	W. . . 3.7	3.3
Sp. . . . 38	=37	51 =29	F. . . . 5.9	5.7
LE. . . 13	=13	15 =9	L. . . . 2.9	3.7
OW. . . 3.2		5.2	R. . . 5–11	5
Cu. . . thin		thin	C. . . . 66	66

X.—Cells of upper epidermis greater in depth; side walls plane, cuticle not ridged (in *M* walls slightly wavy and cuticle slightly ridged on lower surface); palisade deeper sometimes double, midrib structure as in other *X*. In both upper surface rough, hairy (*X* more so); some epidermal cells enormous.—Figs. 18 and 19.

Vessels as in majority. *X*.—Walls of vessels and of fibers very slightly thinner than in *M* and lumina of fibers larger, yet masses of fibers so much more numerous they form more wood; cork and cortical sclerenchyma the same.



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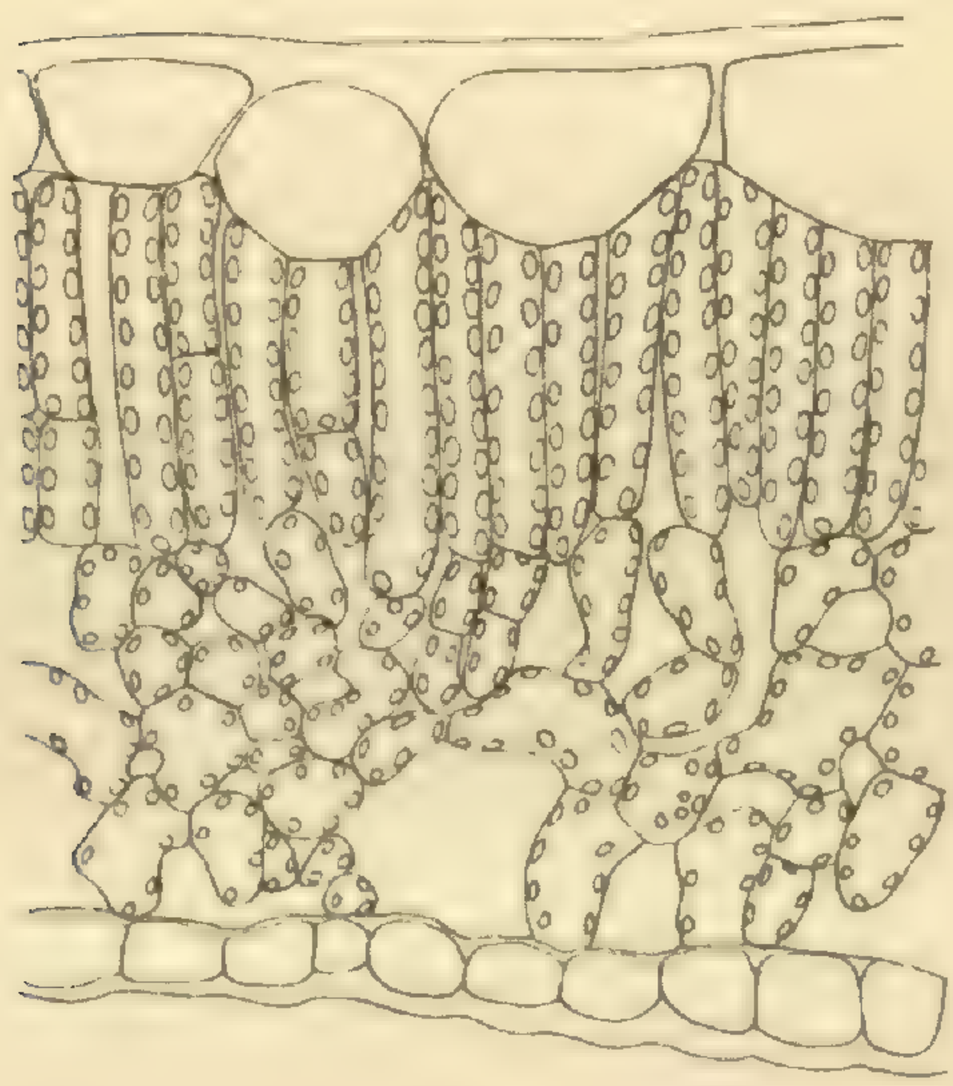


19

FIGS. 18 and 19.—*Ulmus americana:* sections of leaves; fig. 18, mesophytic form; fig. 19, dune form.

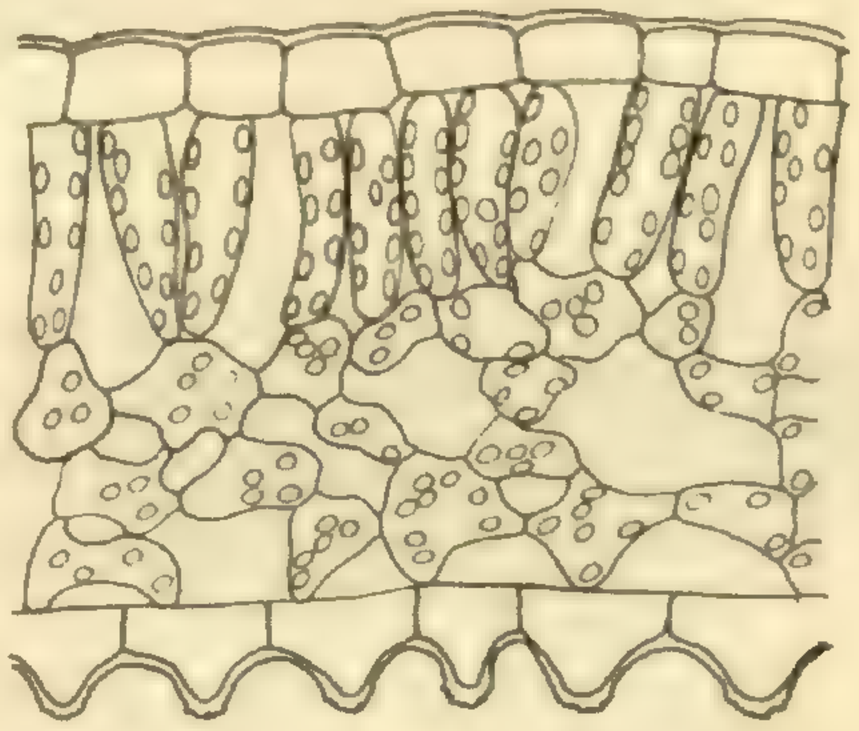
Shrubs

CORNUS STOLONIFERA

	Leaf		Stem	
	M	*X*	*M*	*X*
T.	129 μ (120–144)	156 μ		
UE.	17 = 13 per cent	15 = 10 per cent		
P.	34 = 26	48 = 31		
Sp.	56 = 44	72 = 46		
LE.	22 = 17	21 = 13		
OW.	1.6	2		
Cu.	thin	0.8		
N.			63	70
D.			30 μ (41)	33 μ (45)
W.			3.2	34
F.			4.7	5
L.			6.4	6.2
R.			1–3	2–8
C.			None except at lenticels	112 (in 8-year stem)

X.—Hairs more abundant than in *M*, on upper surface radiating from a center parallel to the surface, tuberculate; on lower surface simple or branched; short hairs also found, formed as slight prolongations of most of the lower epidermal cells, their cuticle prominently ridged; cells of upper epidermis smaller in all dimensions; side walls plane (wavy in *M*); deposits in the form of crystals and oil in the cells, and wax on the outer wall; other points as in most xerophytic forms.—Figs. 20 and 21.

Epidermal cells when present papillate and cuticle heavy; cork not formed before 5 years. In both small groups of sclerenchyma in cortex. All points as in majority.



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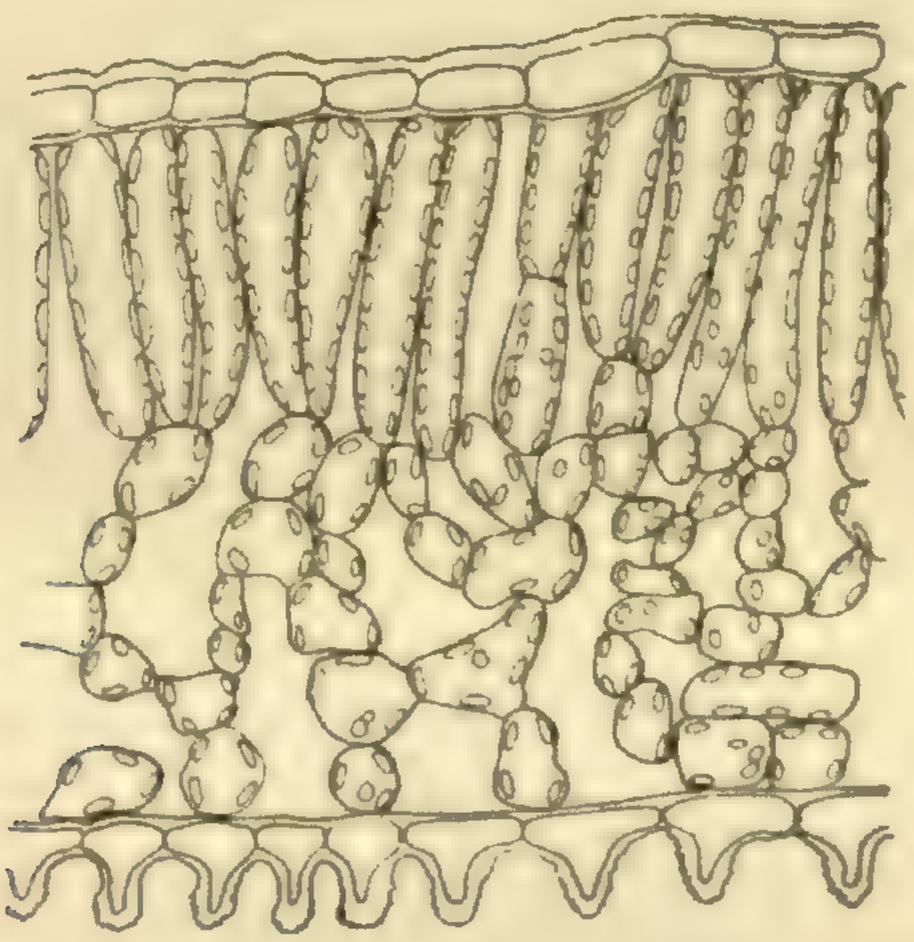
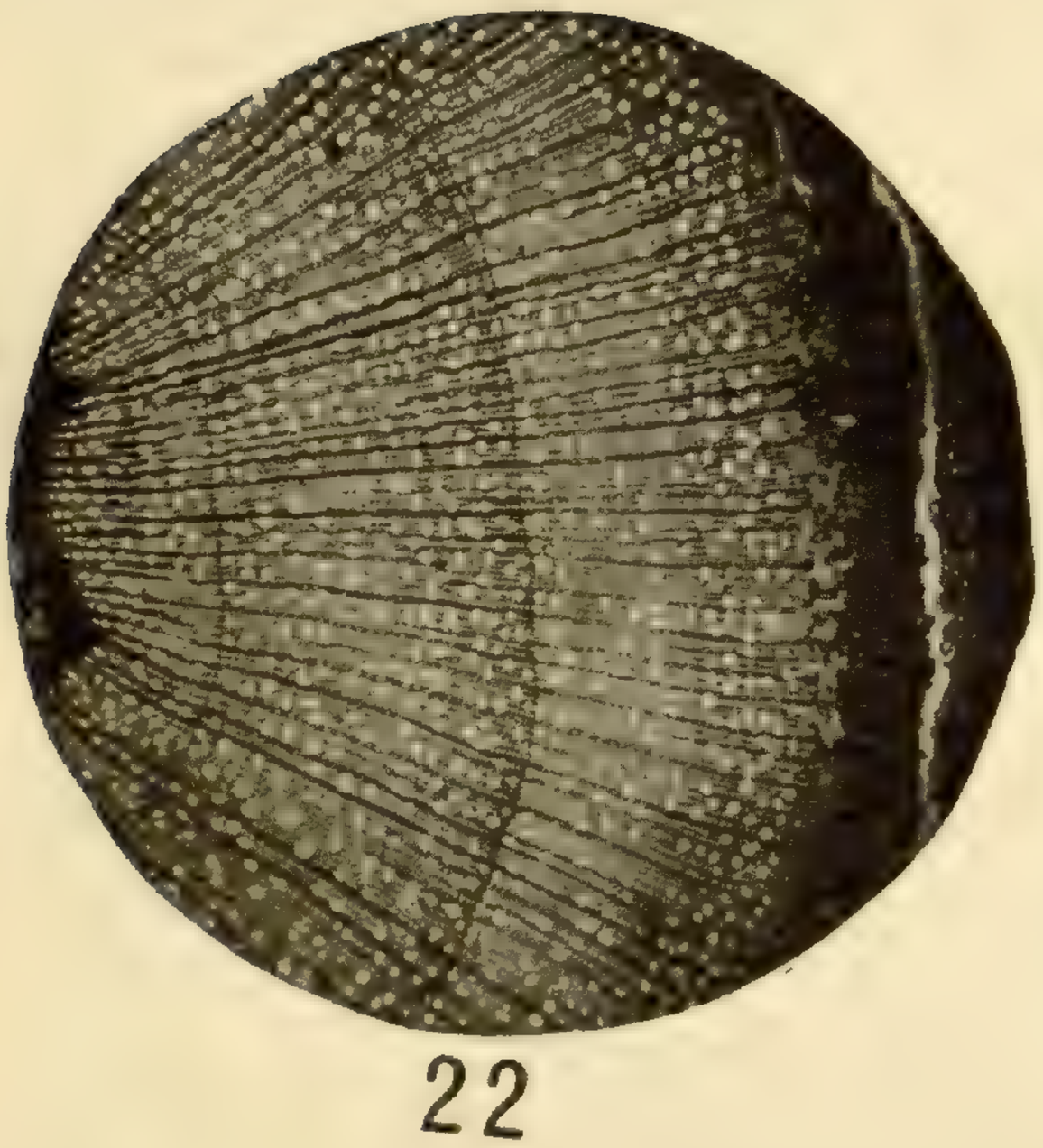


21

FIGS. 20, 21.—*Cornus stolonifera:* sections of leaves; fig. 20, mesophytic form; fig. 21, dune form.

HAMAMELIS VIRGINIANA

	Stem (figs. 22 and 23)	
	M	*X*
N...	94	157
D...	29 μ (37)	24 μ (27)
W...	2.3	1.6
F....	5.7	6.4
L....	5.6	4
R...	3	5
C....	56	48
S....	64	88



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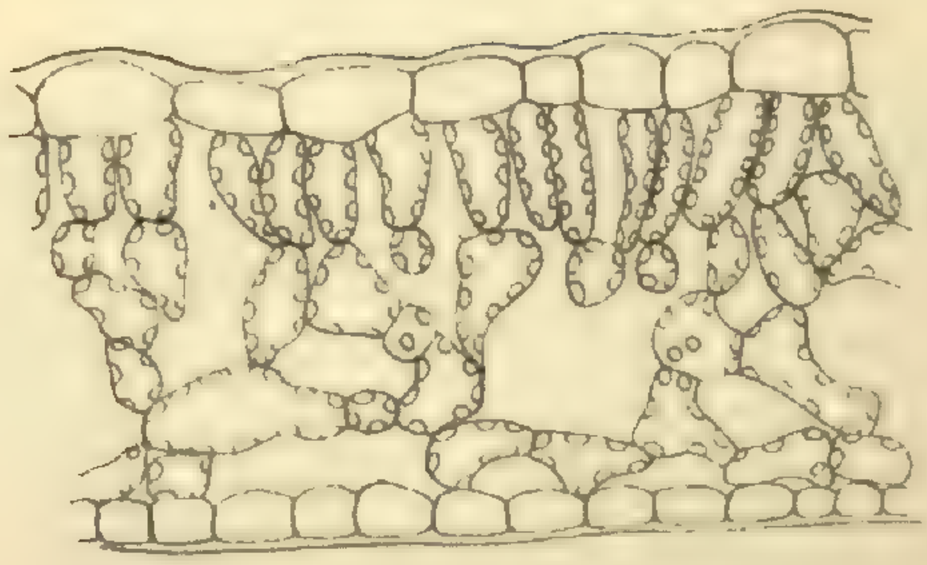

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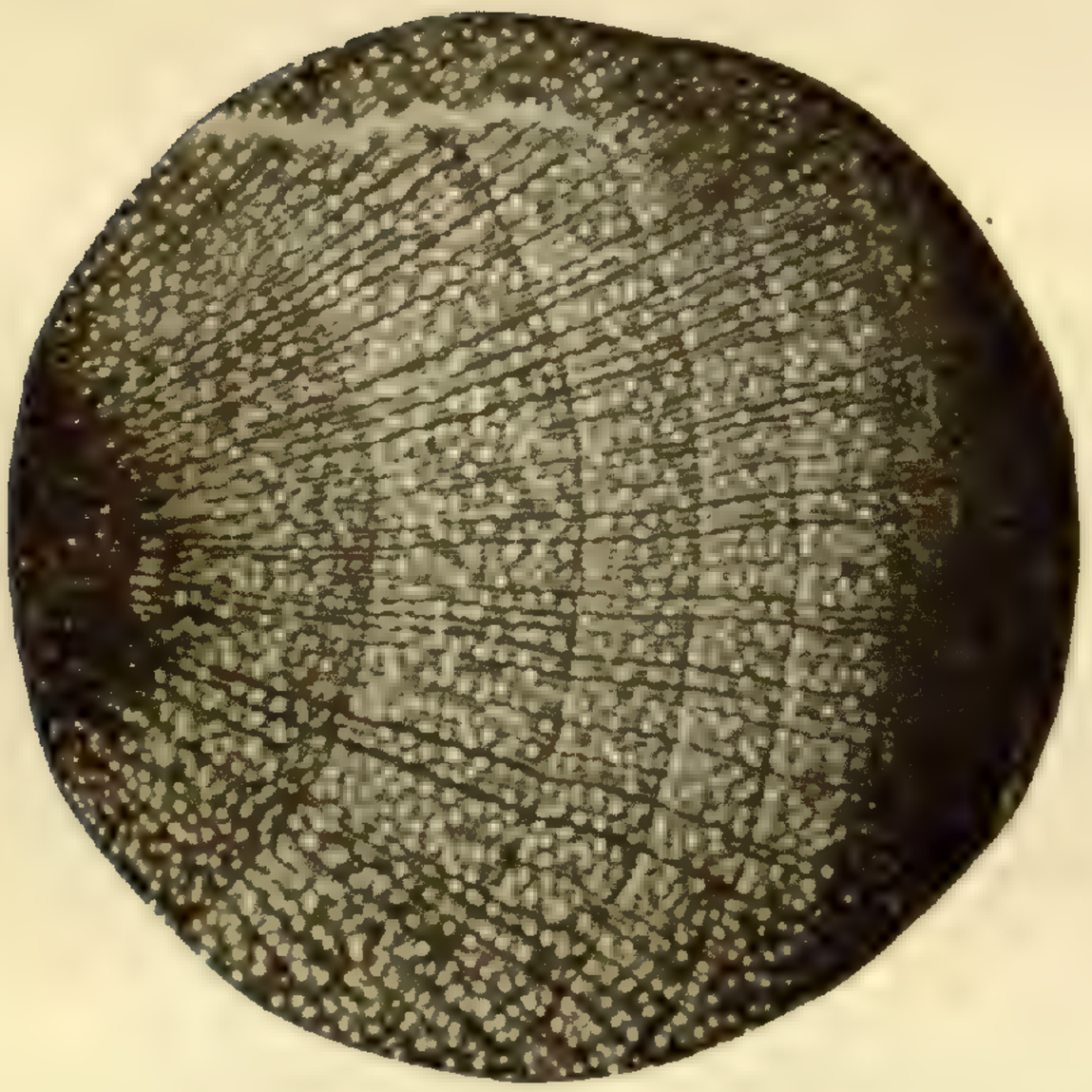

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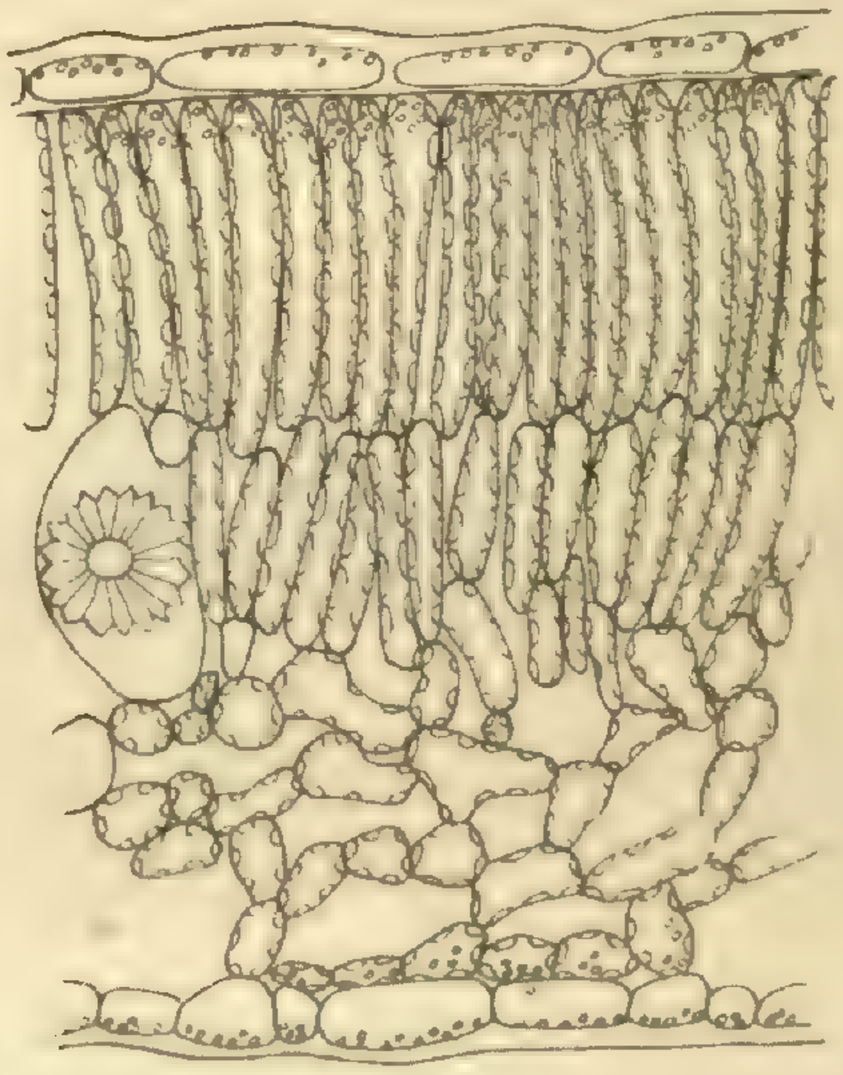


25

FIGS. 22–25.—Figs. 22 and 23, *Hamamelis virginiana:* sections of stems; fig. 22, mesophytic form; fig. 23, dune form; figs. 24 and 25.—*Prunus virginiana:* sections of leaves; fig. 24, mesophytic form; fig. 25, dune form.

PRUNUS VIRGINIANA

	Leaf		Stem	
	M	*X*	*M*	*X*
T.	119 μ (100–123)	198 μ (187–214)	N. 76	108
UE.	18 = 15 per cent	16 = 8 per cent	D. 38 μ (55)	35 μ (45)
P.	35 = 30	99 = 50	W. 3.1	3.5
Sp.	51 = 43	66 = 33	F. 4.6	4.6
LE.	14 = 12	17 = 9	L. 4.7	4.4
OW.	2.9	6.7	R. 3	3–6
Cu.	1.1	1.8	C. 42	61
			S. 83	51

X.—Hairs on lower surface (none in *M*); cells of upper epidermis larger in surface, of less depth, cuticle more prominently ridged than in *M;* side walls less wavy; palisade double (sometimes so in *M*, but cells are not so long nor so compact as in *X*); midrib as in other *X* (sometimes in *M* sclerenchyma below the stele is scarcely perceptible); oil drops, especially in epidermis and upper part of palisade; crystals and other deposits about the bundles.—Figs. 24 and 25.

Only exception to the majority rule is the sclerenchyma, which is heavier in some mesophytic forms.—Figs. 26 and 27.

26

27

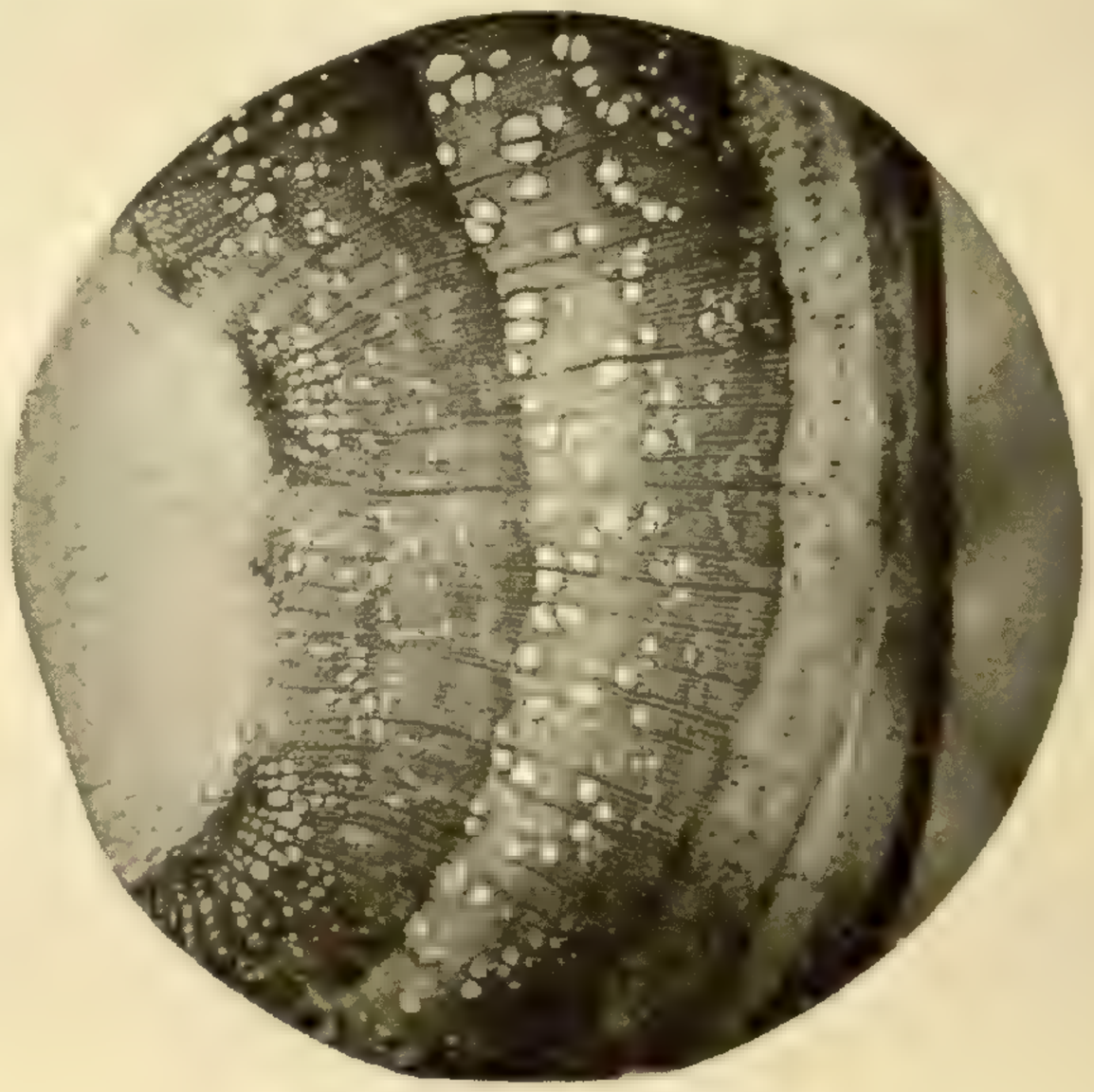
FIGS. 26–27.—*Prunus virginiana:* sections of stems; fig. 26, mesophytic form; fig. 27, dune form.

PTELEA TRIFOLIATA

	Leaf		Stem	
	M	*X*	*M*	*X*
T	147 μ (131–156)	185 μ (177–193)	N 51	51
UE	14 = 9 per cent	18 = 10 per cent	D 53 μ (73)	55 μ (82)
P	42 = 29	56 = 30	W 2.2	3.1
Sp	78 = 53	95 = 51	F 2	2.9
LE	13 = 9	16 = 9	L 8.4	7.2
OW	1.2	4.8	R 2–3	4–7
Cu	thin	1.3	C 50	83

X.—Hairs abundant on lower surface (none in *M*); cells of upper epidermis slightly larger in surface; side walls on both surfaces plane and cuticle ridged (in *M* wavy and only slightly ridged); palisade, sponge, and midrib as in other *X*. One tree in an especially exposed situation, near the top of a wind sweep leading up from the lake, probably once a mesophytic pocket, had a more pronounced structure than the one figured; the leaf averaged 210 μ in thickness, with an outer wall 6.4–8 μ, heavily cutinized.

Agreeing with the majority, except that collenchyma in outer cortex may be no heavier in *X*.—Figs. 28 and 29.



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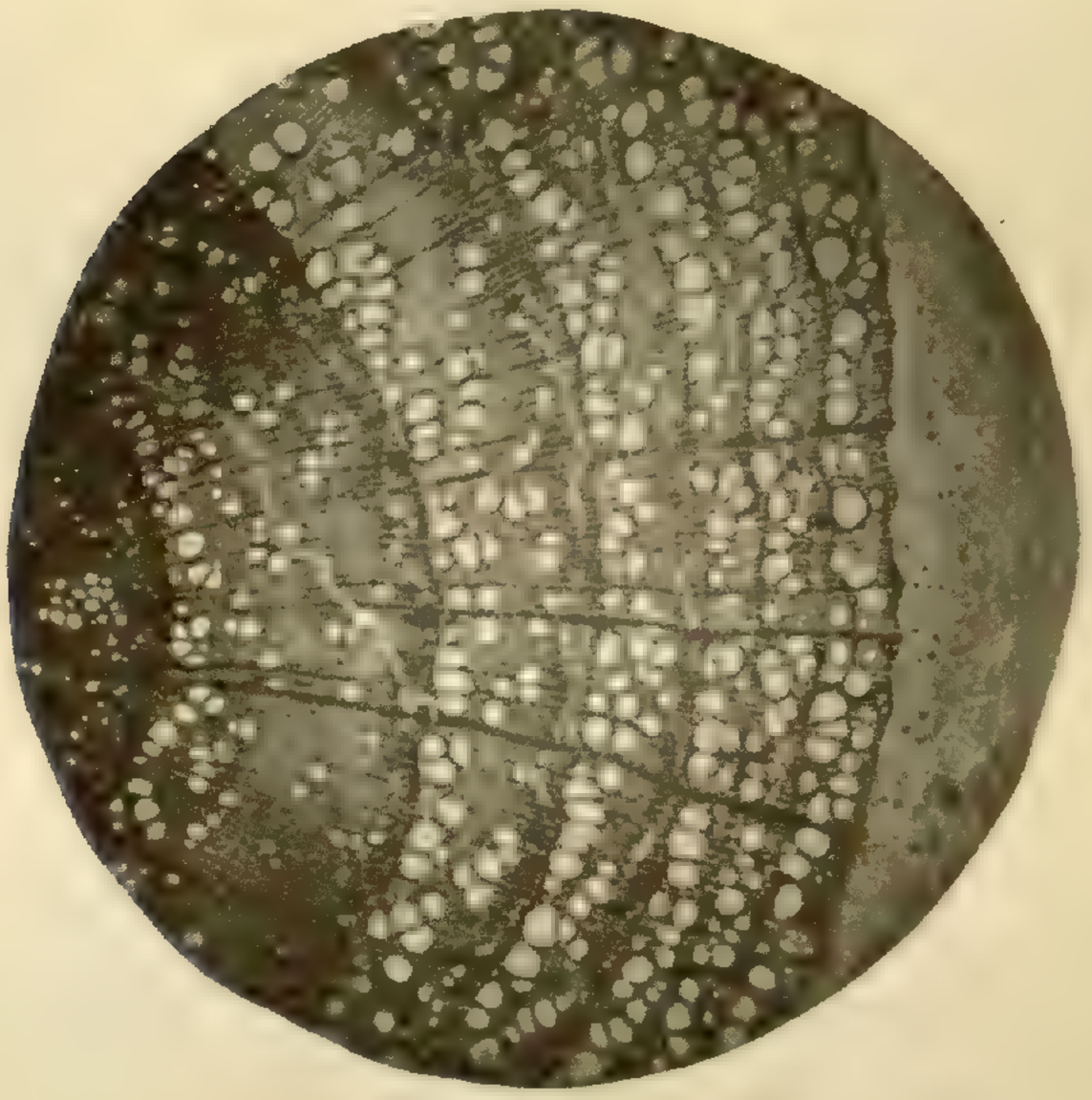


29

FIGS. 28–29.—*Ptelea trifoliata:* sections of stems; fig. 28, mesophytic form; fig. 29, dune form.

SALIX LONGIFOLIA

	Leaf		Stem	
	M	*X*	*M*	*X*
T....	152 μ (136–168)	188 μ (162–212)	N... 77	66.5
UE...	8 = 5 per cent	12 = 6 per cent	D... 36 μ (53)	43 μ (55.5)
Mes..	133 = 88	165 = 88	W... 2.4	2.4
LE...	11 = 7	11 = 6	F.... 2.8	3
OW...	1.5	3	L.... 5.3	6.7
Cu...	thin	2	R... 4	2
			C.... 33	32
			S.... 33	48

Equilateral; two rows of palisade on each side beneath a hypodermis, differentiated as a special storage region; stomata on both surfaces, slightly sunken. *X*.—Upper palisade cells more elongated; sclerenchyma and collenchyma more abundant in midrib.

X.—Agreeing with the majority in the greater area of vessels and greater number and size of sclerenchyma masses in the cortex; exceptional in the larger lumen of the fibers and fewer growth rings.

Lianas

CELASTRUS SCANDENS

	Leaf		Stem	
	M	*X*	*M*	*X*
T.....	101 μ (92–123)	164 μ (138–174)	N... 36	37
UE...	14 = 14 per cent	22 = 14 per cent	D... 54 μ (78)	45.5 μ (69)
P.....	25 = 25	43 = 26	W... 2.8	3.6
Sp....	49 = 48	81 = 49	F.... 4.9	4.5
LE...	13 = 13	18 = 11	L.... 8.4	7.5
OW } Cu }	thin	4 1.7	R... 1–3	1–3
			C.... 80	76

X.—Coarse, often merely acute; veins prominent on the under side. *M*.—Smooth and fine, long acuminate; veins not prominent on under side; other variations as usual.

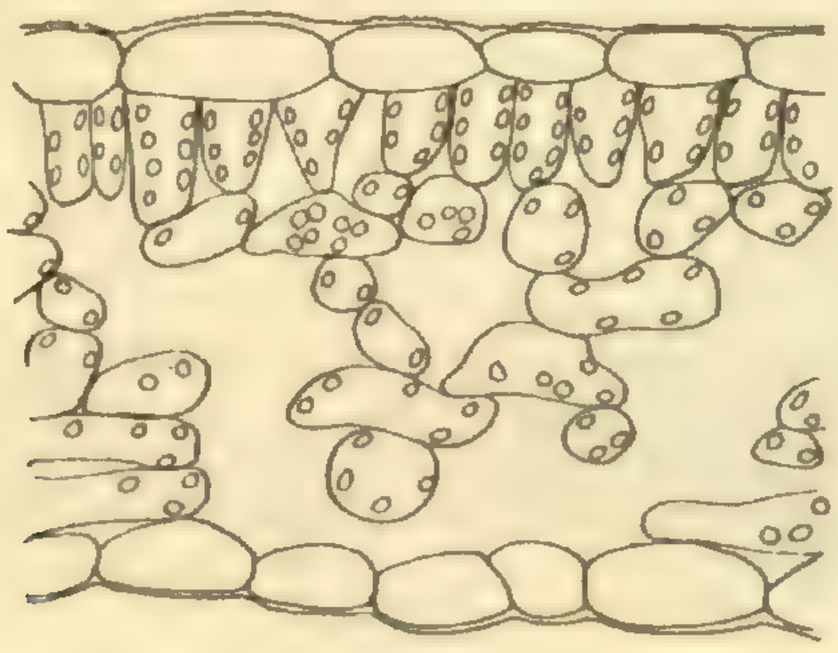
Chiefly an exception; *M* greater in area of vessels, heavier fibers and cork. *X* follows the majority in having heavier sclerenchyma around the pith, thicker walls of the vessels, and smaller lumina in the fibers.

PSEDERA QUINQUEFOLIA

	Leaf		Stem	
	M	*X*	*M*	*X*
T.....	110 μ (99–130)	183 μ (164–195)	N... 36	40.5
UE...	14 =13 per cent	21 =11 per cent	D... 78 μ (120)	61 μ (90)
P.....	24 =22	56 =31	W... 2.8	3.4
Sp....	59 =53	90 =49	F.... 4.6	5.9
LE...	13 =12	16 = 9	L.... 7.2	4.7
OW...	1.5	3	R... 1	1.2
Cu...	0.7	1.5	C....196	188
			S....112	62

In both side walls of epidermal cells plane except in lower surface of *M*, cuticle ridged, hairs on the lower surface. *X*.—Epidermal cells larger in surface, smaller in depth; other points as usual except there is not greater development of conductive tissues.—Figs. 30 and 31.

Exceptional in the smaller area of cross-sections of vessels in *X*, less sclerenchyma and cork; the cork is loose and shreds off, so more may have been lost in *X* than in *M;* the other points agree with the majority.



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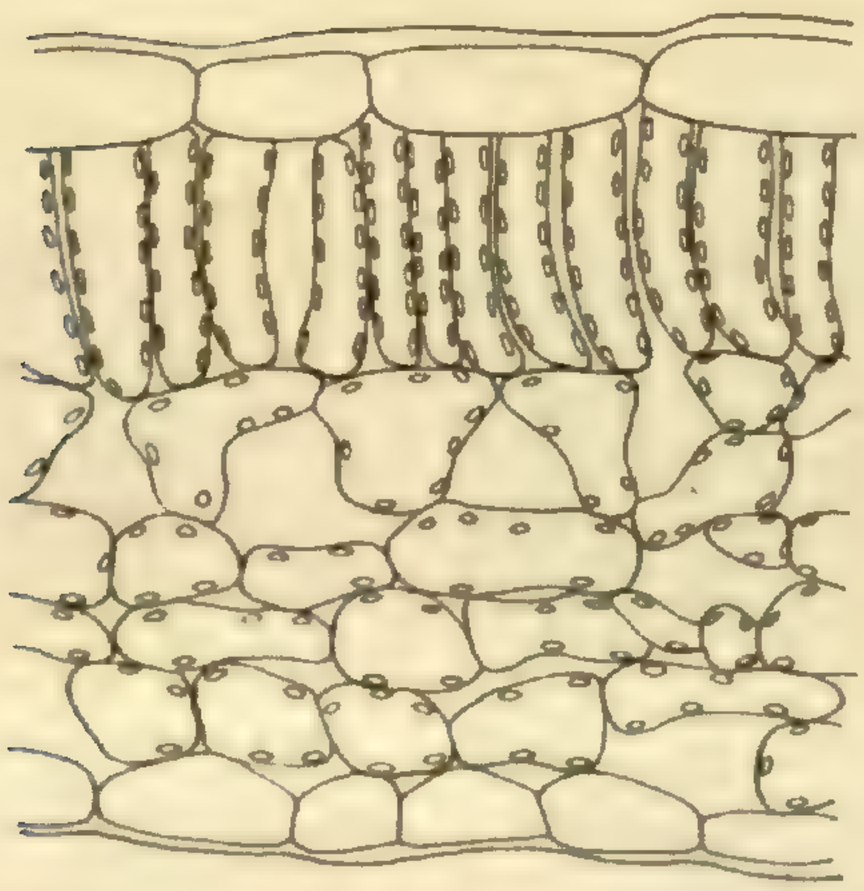


31

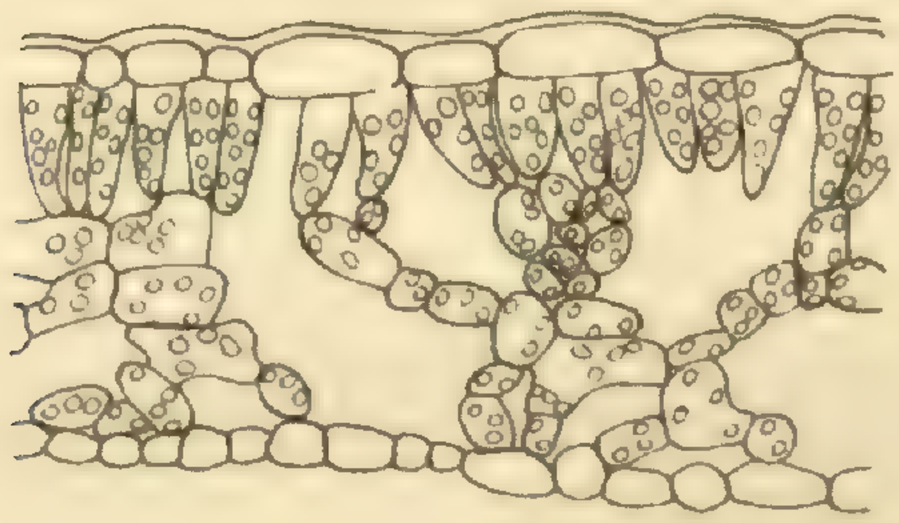
FIGS. 30, 31.—*Psedera quinquefolia:* sections of leaves; fig. 30, mesophytic form; fig. 31, dune form.

RHUS TOXICODENDRON

	Leaf		Stem	
	M	*X*	*M*	*X*
T.....	79 μ (73–116)	140 μ (123–198)	N... 35.5	18.5
UE...	9 =11 per cent	12 = 9 per cent	D... 85 μ (99)	69 μ (88)
P.....	25 =33	45 =32	W... 2	2.4
Sp....	37 =46	70 =56	F.... 2.4	2.8
LE...	8 =10	12 = 9	L..... 9.6	7.2
OW...	1.9	2.7	R... 2	3
Cu...thin		1.4	C....183	145

X.—Epidermal cells smaller in depth; occasional indications of a double palisade; other points as usual.—Figs. 32 and 33.

Exceptional but in the mass of wood formed.



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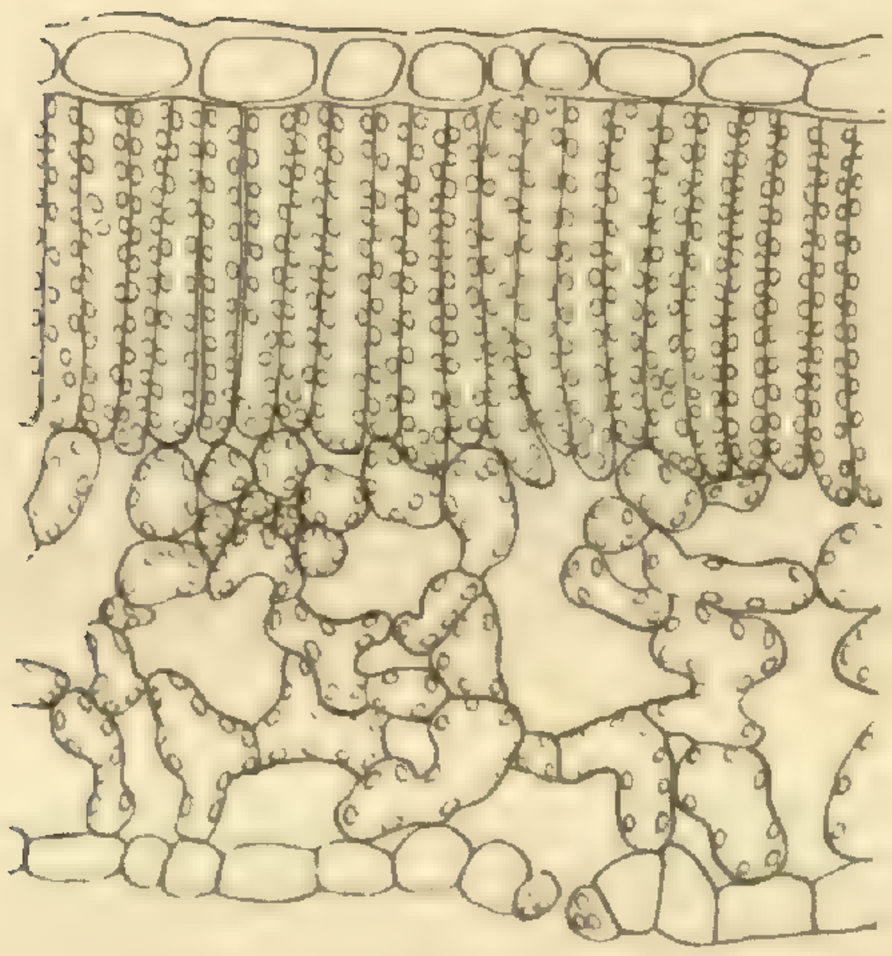


33

FIGS. 32–33.—*Rhus toxicodendron:* sections of leaves; fig. 32, mesophytic form; fig. 33, dune form.

SMILAX HISPIDA

Leaf			Stem (Quadrant used instead of octant)		
	M	*X*		*M*	*X*
T....	106 μ (96–129)	168 μ (157–204)	N...	6 bundles; each with 2 large vessels and 18 smaller	6 2 13
UE...	11 = 11 per cent	22 = 13 per cent			
Mes..	82 = 77	124 = 74			
LE...	13 = 12	22 = 13			
OW...	1.5	3.7	D...	of large vessels	105 107
Cu...	thin	1	W...	4	4
			F....	3.2	3.6
			L....	5.9	4.3
			OW..	18	22

X.—Epidermal cells deeper and larger in surface extent; outer wall and cuticle heavier; cuticle more strongly ridged; side walls less wavy; more conductive and mechanical tissues, but walls thinner. The mesophyll shows the usual monocot variation, no differentiation into palisade and sponge.

X.—Two vessels larger, but not so many small ones; cortex more collenchymatous; pith cells with thicker walls, pith packed with starch grains and crystals.

VITIS VULPINA

Leaf			Stem		
	M	*X*		*M*	*X*
T.....	105 μ (100–118)	153 μ (127–164)	N...	9	10
UE...	14 = 13 per cent	13 = 9 per cent	D...	105 μ (142)	102 μ (127)
P.....	28	45 = 29	W...	4	4.5
S.....	50	81 = 53	F....	5.2	4.8
LE...	13	14 = 9+	L....	7.2	7.1
OW	thin	1.8	R...	2–3	2–3
Cu	thin	1	C....	236	307

X.—Upper epidermal cells smaller in depth, larger in surface; hairs on veins on both surfaces (only on upper in *M*); other points as usual. In both walls plane and cuticle somewhat ridged.

X.—Slightly more area in cross-sections of vessels; cork thicker; less sclerenchyma.

Herbs

ASCLEPIAS SYRIACA

	Leaf		Stem	
	M	*X*	*M*	*X*
T.	225 μ (230–296)	272 μ (237–304)		
UE.	25 = 10 per cent	25 = 9 per cent		
P.	54 = 21	77 = 28		
Sp.	158 = 62	151 = 56		
LE.	18 = 7	19 = 7		
OW.	2.4	2.4		
N.			25	18
D.			46 μ (66)	64 μ (87)
W.			3.5	4.6
F.			2.9	3.5
L.			17	15
OW.			4	6.4
Wood cyl			185	611

In both side walls of upper epidermal cells plane, of lower wavy; cuticle ridged on lower surface. *X*.—Hairs on both surfaces (only on lower in *M*); upper epidermal cells smaller in depth, larger in surface; palisades often deep in proportion to sponge; where not, a secondary palisade partly organized; conductive and supporting tissues as usual; latex and other secretions more abundant.—Figs. 34 and 35.

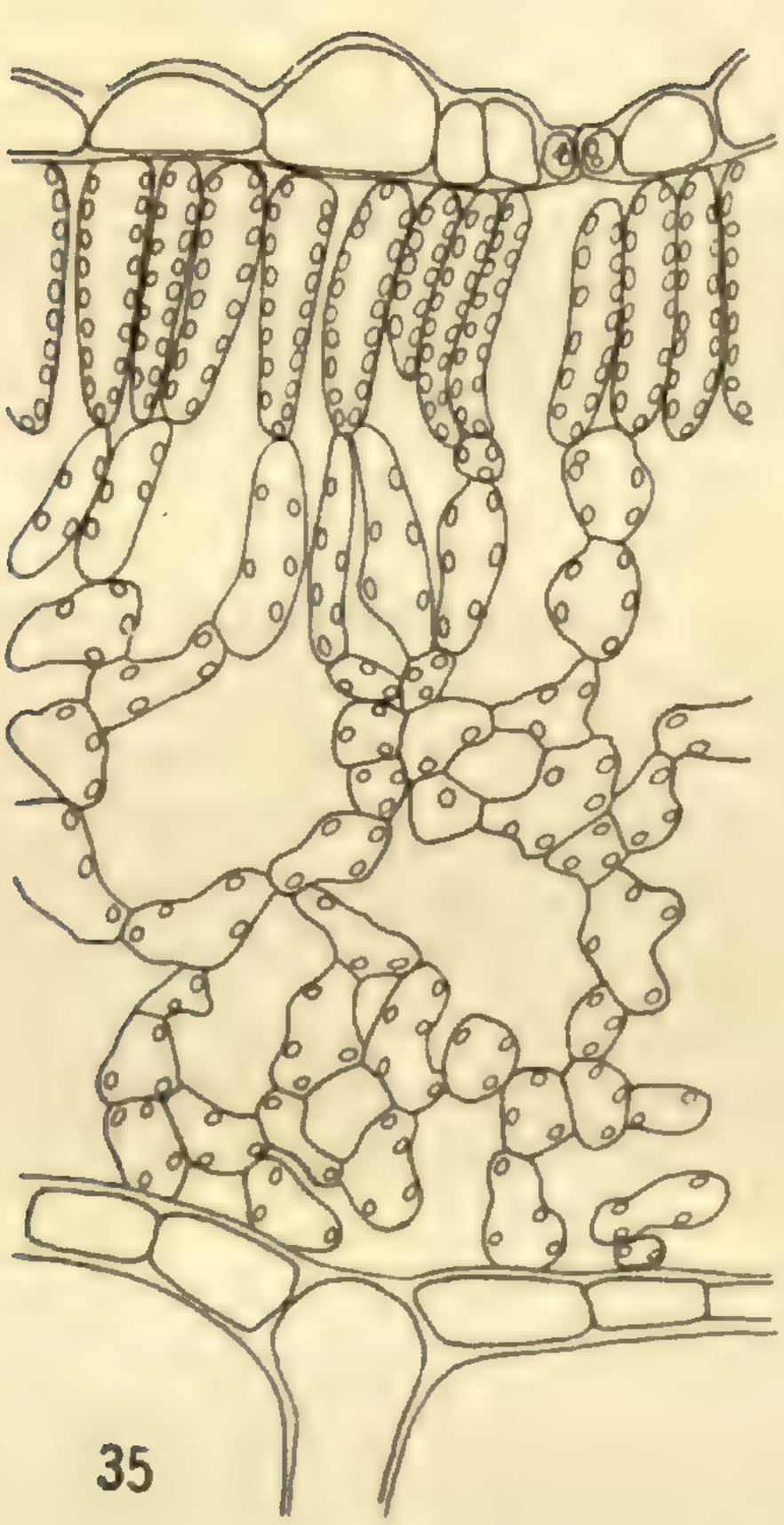
X.—Area of cross-sections of vessels smaller, larger cylinder of wood formed; walls of vessels and of fibers heavier, lumen of fibers smaller, so more wood; outer wall of epidermis and hypodermal collenchyma heavier.

SMILACINA STELLATA

	Leaf		Stem	
	M	*X*	*M*	*X*
T.	174 μ (155–199)	202 μ (182–242)		
UE.	28 = 16 per cent	30 = 15 per cent		
M.	119 = 68	144 = 71		
LE.	27 = 16	29 = 14		
OW.	2.6	2.9		
Cu.	0.7	0.7		
Bundles in field			12	12
N in bundle			15	13
D.			27 μ	32 μ
W.			4.3	4.5
OW.			7.2	6.4

X.—Epidermal cells smaller in depth, larger in surface; hairs more abundant, more crystals deposited; other variations as usual; in both no differentiation in the mesophyll, the general monocot situation; side walls of epidermal cells plane.

X.—Area of cross-sections of vessels greater; walls of vessels heavier, but outer wall thinner.



FIGS. 34, 35.—*Asclepias syriaca:* sections of leaves; fig. 34, mesophytic form; fig. 35, dune form.

Swamp forms

Sometimes a moving dune passes over a swamp association, and the members by increased length of stem keep pace with it for a time; a few of these have been examined and compared with forms growing in their natural habitat.

PLATANUS OCCIDENTALIS

	Leaf		Stem	
	S	*X*	*S*	*X*
T.	152 μ (136–162)	199 μ (162–205)		
UE	23 = 15 per cent	25 = 12 per cent		
P.	52 = 34	63 = 32		
Sp.	62 = 41	92 = 46		
LE.	16 = 10	19 = 10		
OW	4	2.8		
N.			66	69
D.			35 μ (50)	46 μ (63)
W.			3.2	3.2
F.			5	3.2
L.			6.4	7
R.			3	2
C.			68	6.9
S.			100	116
Collen			56	109

The dune form has thicker leaves than the swamp form, but the palisade and outer wall of the epidermis are exceptional.

The dune form shows an increase in number and size of the vessels, but there is no increase in woody tissue furnished by the fibers. There seems to be no diminution in growth as indicated by the growth rings, but mechanical tissue outside the stele and the cork have increased.

ALNUS INCANA

	Stem	
	S	*X*
N.	68	61
D.	29	34
W.	2.5	2.6
F.	3.5	3.4
L.	7	8.8

Swamp form, vessels larger than the others but fewer in number. Dune form, larger area of vessels. Thickness of walls about the same.

CEPHALANTHUS OCCIDENTALIS

	Leaf	
	S	*X*
T.	175 μ (143–168)	163 μ (147–189)
UE	16 = 9 per cent	17 = 10 per cent
P.	54 = 31	48 = 29
Sp.	91 = 52	84 = 52
LE.	14 = 8	14 = 9
OW	3	3.7
Cu.	1.6	2

A second layer of palisade is partly organized in the swamp form and completely in the dune form. The first palisade is relatively shorter in the dune form, but the second is so much more compact than in the swamp form that it must more than make up the amount of tissue. In both forms stomata are found on the lower surface only and the side walls of the epidermal cells are waxy.

SALIX GLAUCOPHYLLA

	Leaf		Stem	
	M	*X*	*S*	*X*
T....	185 μ (180–208)	231 μ (219–240)		
UE...	20 = 10 per cent	19 = 9 per cent		
P....	92 = 50	120 = 52		
Sp....	57 = 31	69 = 30		
LE...	16 = 8	19 = 9		
OW...	4.3	4.8		
Cu...	1.6	1.6		
N....			57	64
D....			45	47
W....			2.3	2.4
F....			3.1	4.8
L....			5	3.2
R....			2–4	4
Cork..			56	80
Collen			4–6 layers	7 layers

Little variation, but the palisade is slightly deeper in the dune form; the vessels of the midrib are larger though about as numerous, their walls are heavier as is also the outer epidermal wall, and there is more collenchyma.

In the dune form more vessels and larger; the fibers heavier and the lumina smaller, giving more wood; growth rings about the same; more cork, collenchyma, and sclerenchyma.

CORNUS STOLONIFERA

A plant growing on the edge of a river was partly submerged by a dune. The stem was examined to find the difference between the submerged and the aerial parts.

	Submerged	Aerial
Cortex and phloem	400 μ	380 μ
Wood cylinder	836	950
Pith	1976	1482
	3212	2812

The upper exposed part is not as large as the submerged part, but the wood cylinder is larger.

	Submerged	Aerial
N	62	44
D	23	38
W	2.3	3.2
F	5.1	5.6
L	10.4	5.6

In a given area in the cylinder there are fewer vessels, larger in diameter but less in area, which must be more than compensated for by the size of the whole cylinder. The walls of the vessels and fibers are heavier and the lumina of the fibers smaller, giving more wood.

SALIX LONGIFOLIA

Situation the same, but the parts examined were not parts of the same stem, but were of the same size.

	Submerged	Aerial
N	42	51
D	41	43
W	3.2	2.4
F	3	3.2
L	7.7	6.8

In aerial stem more and larger vessels, walls slightly thicker, lumina of fibers smaller, giving more wood.

The swamp forms on the whole show the same variations as the mesophytic forms.

Table (I) on p. 298 gives a comparison of mesophytic and dune forms of the same species with respect to eleven characters of the leaf.

A summary of leaf characters is as follows:

Hairs more abundant	12 *X*	(3 same)
Surface of upper epidermal cells greater	9 *X*– 5 *M*	(2 same)
Depth of upper epidermal cells greater	5 *X*–12 *M*	(4 same)
Side walls of upper epidermal cells wavy	6 *X*–11 *M*	
Side walls of lower epidermal cells wavy	8 *X*–16 *M*	
Outer wall of epidermis heavier	18 *X*	(2 same)
Cuticle ridged	10 *X*– 6 *M*	
Palisade more completely organized	17 *X*	(1 same)
Better development of conductive elements	15 *X*– 2 *M*	(1 same)
Heavier sclerenchyma	14 *X*– 1 *M*	(1 same)
Heavier collenchyma	17 *X*	

All leaves, with the exception of those of *Populus balsamifera*, were thicker in the dune form than in the mesophytic. The poplar was growing alone at the side of a road, so the exposure was greater than in the woods where most of the mesophytic specimens were collected. The bud scales also were thicker, and in most cases the outer wall, or the cork if it had developed, was thicker.

The greater extent of surface in the upper epidermal cells in the majority of the dune forms is striking. GREVILLIUS speaks of epidermal cells in the alvar plants being smaller than in the normal, but he may have used the lower surface only, as he mentions the subject in connection with stomata, and that may differ from the upper surface. Cuticular transpiration is reported as taking place from the side walls of the epidermal cells more abundantly than from the lumen of the cell. If this is true, then increase in the surface extent of the cell would decrease cuticular transpiration. The apparent thickness of the epidermis of dune forms is due to the heavy wall and cuticle and not to the depth of the cells. Waviness of the side walls seems to be related to shade, as it occurs more frequently in mesophytic leaves, and in mesophytic leaves on the under side. Ridging of the cuticle accompanies great thickness. Deep, compact palisade, well developed conductive elements, heavy sclerenchyma, and the presence of hairs are characters noted

TABLE I

LEAF CHARACTERS OF MESOPHYTIC AND DUNE FORMS COMPARED

	Acer	Asclepias	Celastrus	Celtis	Cornus	Fraxinus	Juglans	Liriodendron	Ostrya	Populus balsamifera	Populus deltoides	Prunus virginiana	Psedera	Ptelea	Rhus	Salix longifolia	Smilacina	Smilax	Tilia	Ulmus	Vitis
Hairs more abundant	*x*	*x*	*o*		*x*	*x*	*x*	*o*		*mx*	*x*	*x*	*mx*	*x*	*x*	*o*	*x*	*o*	*mx*	*x*	*x*
Surface of epidermal cells absolutely greater	*mx*	*x*	*x*		*m*	*m*	*mx*	*m*			*m*	*x*	*x*	*x*			*x*	*x*	*x*	*m*	*x*
Depth of epidermal cells relatively greater	*m*	*m*	*mx*	*mx*	*m*	*x*	*m*	*m*	*m*	*x*	*mx*	*m*	*m*	*mx*	*m*	*x*	*m*	*x*	*m*	*x*	*m*
Side walls of upper epidermal cells wavy	*mx*	*o*	*mx*	*m*	*m*	*mx*	*m*	*m*		*o*	*o*	*mx*	*o*	*m*			*mx*	*mx*	*o*	*m*	*o*
Side walls of lower epidermal cells wavy	*mx*	*mx*	*mx*		*m*	*mx*	*m*	*m*		*m*	*o*	*mx*	*m*	*m*			*mx*	*mx*	*m*	*m*	*mx*
Outer walls of epidermis (including cuticle) heavier	*x*	*mx*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*mx*	*x*	*x*	*x*	
Cuticle ridged	*x*	*mx*			*x*	*x*				*x*		*x*	*m*	*mx*				*x*	*mx*	*m*	*mx*
Palisade more completely organized	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*		*x*	*x*	*x*	*x*	*x*	*mx*			*x*	*x*	*x*
Better development of conductive elements		*x*	*x*	*x*	*x*	*x*	*x*	*x*		*x*	*x*	*x*	*m*	*mx*	*x*		*x*	*m*	*x*	*x*	*mx*
Heavier sclerenchyma	*x*					*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*m*	*mx*	*x*	
Heavier collenchyma		*x*	*x*	*x*	*x*	*x*	*x*	*x*			*x*	*x*		*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*

in true dune plants and generally admitted to be xerophytic. Stomata appear only on the under sides of leaves of both forms except in the cases noted, where they appear on both sides; there is no variation except in the one tree *Ostrya* which sometimes has stomata on the upper surface also. Occasionally specimens from mesophytic situations in the dunes show interesting variations. In these places a great deal of humus has collected above the sand, changing the water content and other soil relations, and xerophytic pioneers have made enough shade and protection for mesophytic forms to come in, so woods have developed. The exposure must be less here and the water relations better than on dunes with scantier vegetation, yet leaves of *Fraxinus*, *Cornus*, and *Ostrya* collected in these woods were thicker than some of the dune forms. The internal structure of *Fraxinus* differed from the dune form, the palisade consisting of a single layer of cells, not compactly arranged.

Another interesting variation comes out in the comparison of leaves of different seasons. Those collected in 1911 are frequently thicker than those collected in 1909 in the same habitat, so that the mesophytic form of 1911 is sometimes thicker than the xerophytic form of 1909, but the xerophytic form of 1911 is correspondingly increased. The season was an unusual one, showing temperatures of 39°, 46°, and 66°, for March, April, and May, in which time the leaves became fully mature, the normal being 34·4°, 45·9°, and 56.5°. In 1909 the temperature was very near the normal. The normal percentages of possible sunshine are 52, 60, and 64, while 1911 had 63, 54, and 79, so March and May were considerably above the average, though April went below. Precipitation was near the normal except in March, when it was only a little more than half. Winds were not unusually high. The variation in thickness must have been due, at least in part, to the unusually high temperature in the three months, sunshine above the average in March and May, and small precipitation in March.

The accompanying table (II) gives a comparison of mesophytic and dune forms as to nine characters of the stem.

TABLE II

STEM CHARACTERS OF MESOPHYTIC AND DUNE FORMS COMPARED

	Acer	Asclepias	Celastrus	Celtis	Cornus	Fraxinus	Hamamelis	Juglans	Liriodendron	Ostrya	Populus balsamifera	Populus deltoides	Prunus virginiana	Psedera	Ptelea	Rhus	Salix longifolia	Smilacina	Smilax	Tilia	Ulmus	Vitis
Vessels more numerous	*m*	*m*	*x*	*x*	*x*	*m*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*mx*	*m*	*m*	*m*	*m*	*x*	*x*	*x*
Vessels larger	*x*	*x*	*m*	*mx*	*x*	*m*	*m*	*m*	*m*	*m*	*m*	*x*	*m*	*m*	*x*	*m*	*x*	*x*	*x*	*x*	*mx*	*m*
Total area of vessels larger	*x*	*m*	*m*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*m*	*x*	*m*	*x*	*m*	*x*	*x*	*x*	*x*
Walls of vessels heavier	*x*	*x*	*x*	*x*	*x*	*x*	*m*	*x*	*x*	*m*	*m*	*x*	*x*	*x*	*x*	*x*	*mx*	*mx*	*x*	*x*	*m*	*x*
Walls of wood fibers heavier	*x*	*x*	*m*	*x*	*x*	*x*	*x*	*m*	*x*	*x*	*m*	*x*	*mx*	*x*	*x*	*x*	*x*	*x*		*m*	*m*	*m*
Lumen of fibers smaller	*m*	*x*	*x*	*x*	*x*	*mx*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*m*	*x*		*x*	*m*	*mx*
More growth rings in stem of given size	*m*		*m*	*mx*	*x*	*m*	*x*	*mx*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*m*			*mx*	*m*	*x*
More sclerenchyma and collenchyma	*m*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*m*	*m*	*x*	*x*	*x*	*m*	*x*	*m*	*mx*	*m*
Cork thicker	*m*		*m*	*m*	*x*	*x*	*m*	*m*	*x*	*x*	*x*	*x*	*x*		*x*	*m*	*m*			*m*	*mx*	*x*

A summary of stem characters is as follows:

Vessels more numerous	14 *X*– 7 *M* (1 same)
Vessels larger	9 *X*–11 *M* (2 same)
Total area larger	17 *X*– 5 *M*
Walls of vessels heavier	16 *X*– 4 *M* (2 same)
Walls of fibers heavier	14 *X*– 6 *M* (1 same)
Lumen of fibers smaller	16 *X*– 2 *M* (2 same)
More growth rings	10 *X*– 6 *M* (3 same)
More sclerenchyma and collenchyma	15 *X*– 6 *M* (1 same)
Cork thicker	9 *X*– 8 *M* (1 same)

There is a tendency for the vessels to be larger in the mesophytic forms, but more numerous in the xerophytic, the area being greater in the xerophytic. A greater number of xerophytic forms have heavier walls of vessels and fibers and smaller lumen in the fibers, making a more woody cylinder. A majority of xerophytic forms have more growth rings to the given diameter than the mesophytic forms, showing slower growth under the more adverse conditions. A majority of xerophytic forms show an increase in mechanical tissue as well as in the wood and an increase in cork formation, though this is not so marked as one might expect. The internodes in the stem, in every case measured, were shorter in the xerophytic form.

The lianas seem more apt than the trees to show exceptions to the general stem situation. Their vessels are always extraordinarily large, but why they should often be larger and more numerous in mesophytic forms, when those of trees are not, is impossible to guess.

Discussion of theories

That the characters cited are due to the conditions under which the plants live, or have lived in the past, is undoubted, but what are the immediate causes remains to be proved by experiment. The purpose of this investigation has been to get at a few facts, but it may be of some interest to review a few of the theories:

Mrs. CLEMENTS (**4**) considered light the principal factor in the development of deep palisade. HABERLANDT (**16**) said that light does not influence the structure of this tissue but only its disposition, and that the reason palisade is developed is because

the products of assimilation ought to be carried away from the assimilatory cells by the shortest possible road, and the form of cells best fitted for this rapid transportation is the elongated form. WAGNER (**29**) reported that alpine plants exposed to decreased transpiration did not show a reduction in palisade, and concluded that not transpiration but assimilation was more effective in producing that tissue. PICK (**25**) thought the elongated form of the palisade is ancestral, but that for a strong development light is necessary; DUFOUR (**9**) agreed with him in this respect. STAHL (**26**) related palisade development to light. EBERDT (**10**) thought that increase in palisade development is caused by assimilation and transpiration working together, and that light in itself is never the cause that calls forth palisade parenchyma. VESQUE and VIET (**27**) concluded from their experiments that light and dry air (accelerating transpiration) result in a greater development of palisade. BONNIER (**2**) adds temperature to these two factors. KEARNEY (**22**) considers excessive transpiration accountable for both increased palisade and succulency. HEINRICHER (**20**) related equilateral structure to the vertical position of leaves and thought it due to sunny and dry situations, dryness being secondary to strong illumination, as some plants growing in damp situations have equilateral leaves.

As to conductive and mechanical elements, it has long been known that they are reduced in aquatic plants, in the water leaf of *Proserpinaca* being scarcely differentiated at all. If the supply of water is the limiting factor, one would expect an increase in these tissues the more xerophytic the conditions; but of course water is not the only factor, and with the plant out of water, its roots in the soil, its leaves in the air, the larger the plant, and consequently the farther apart the roots and leaves, the more complicated become the factors. GILG (**14**) found in the xerophytic family Restiaceae a mechanical ring of strongly thickened cells, which VOLKENS (**28**) explained as related to poor water supply. HABERLANDT (**17**) thought mechanical influences, if they do not pass beyond a certain limit, act on stereome as a stimulus for further building it up. KOHL (**23**) found that in some plants grown in damp air the sclerenchyma ring was entirely lost, xylem elements

less numerously developed, and bast bundles weak or gone, due, he said, to differences in activity of transpiration. JOST (**21**) found that in *Phaseolus* a great mass of vessels was formed, even if transpiration was reduced to the minimum, and says "transpiration can indeed influence the quality and quantity of the vessels, but is not the cause of their formation. If it were so, the stems of our trees would grow in thickness as long as they transpire, at least the whole summer through, which they do not do." HABERLANDT (**18**) relates the number and size of the ducts to the transpiring leaf surface. HARTIG (**19**) agrees with HABERLANDT and adds "in the damp air of a dense forest the inner spaces are much narrower than in an open stand." PFEFFER (**24**) considers that within certain limits the development of the conducting system is favored when an increased demand is made upon it. VOLKENS (**28**), in studies of desert plants, found a small development of water-conducting elements. CANNON (**5**) irrigated desert plants and compared their ducts with those of non-irrigated plants and found better development in the latter. The two results may not be inconsistent. VOLKENS' plants may have reduced leaf surface or developed succulency, thus reducing transpiration, and so in a way correspond with CANNON'S irrigated plants.

Conclusions

Conditions in the dunes are severe for plant life, including direct illumination and reflection, extremes of temperature, strong winds, sand-blast, and sandy soil, the result of all these factors being increased evaporation. The presence of considerable water above the water-table makes conditions less severe than they otherwise would be. The response to these conditions by true dune plants is seen in the predominance of low vegetation, long roots, woody stems, thick leaves (which may be reduced, equilateral, evergreen, or folded), succulency, hairs, thickened epidermis and cuticle, deep palisade, sunken stomata, and well developed mechanical and conductive tissues in all parts.

Plants generally growing in mesophytic situations, when found also on the dunes, show the following modifications: *of the leaf*, increased thickness, decrease in depth and increase in surface-

extent of epidermal cells, increase in thickness of the outer wall of the epidermis and of the cuticle accompanied by ridging, increase in palisade, in hairs, in conductive and mechanical tissues; *of the stem*, decrease in the length of internodes, increase in the number of vessels and in the area of their cross-sections, giving greater conductive space, increase in thickness of the walls of vessels and of the fibers accompanied by decrease in lumen of fibers, giving more wood, increase in the number of growth rings in stem of a given size, showing slowness of growth, increase in mechanical tissues outside the wood, and increase in cork.

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PARNASSIA AND SOME ALLIED GENERA

LULA PACE

(WITH PLATES XIV–XVII)

The systematists have had some trouble in classifying *Parnassia*. In an old Westphalian Flora by KARSCH (**15**) it is placed in the family Droseraceae. HALLIER (**12**), in discussing the Saxifragaceae, says *Parnassia* is much more closely related to the Droseraceae than to the Saxifragaceae; while EICHINGER (**6**) concludes that it should be placed with the Saxifragaceae as ENGLER (**8**) has it. WETTSTEIN (**26**) also places it there and takes Droseraceae out of the Sarraceniales and puts it with Parietales. The possibility of finding some characteristics that would help settle this question led to the present study. CHODAT (**3**) has used *Parnassia* to illustrate certain stages in the development of the embryo sac and embryo of angiosperms.

The work was undertaken at the suggestion of the late Professor STRASBURGER, and his continued advice was of the greatest service.

Parnassia palustris

MATERIAL.—The material which had been collected in Switzerland, and in the neighborhood of Bonn, Germany, was kindly placed at my disposal by Professor STRASBURGER. It had been killed in an alcohol acetic mixture (three parts of alcohol to one part of glacial acetic acid). The usual methods were followed in preparing the material for cutting. The younger stages were cut 5–6 μ thick and the older 8–10 μ. The triple stain, safranin-gentian violet-orange G, was most satisfactory, but iron-alum hematoxylin alone and with Congo red was also used.

The parts studied showed very few irregularities, or so-called abnormalities. Out of several hundred ovaries sectioned, the majority had five placentae, a few had four, two had three, and one had only two; in the last the two placentae were not quite normal in appearance. One ovary had a very irregular structure; it was as if the carpels had not grown together, and more or less

perfect anthers, containing apparently normal pollen, were found on these (fig. 70). One anther had developed on a staminodium; two anthers were normal in appearance. CHAMBERLAIN (**2**) has reported certain somewhat similar irregularities in anther development in *Salix*.

MEGASPORES.—A complete series in the development of the ovule from the first protuberance was studied. The earliest stages show no differentiation of sporogenous tissue. The first difference to be noted is in ovules that are somewhat advanced; and these show only a difference in the size of the cells, there being no definite arrangement of these and no difference in staining reaction. Certain characteristic groups of these larger cells are shown in figs. 1, 2, and 3; the first two are from the same section. Often there are only two large cells, as may be seen in fig. 1, but in this case a third cell is below these two. Fig. 2 has four large cells that evidently were produced from one cell by two successive divisions, thus giving a rather striking resemblance to four megaspores; the wall between the two upper cells is very faint. At this stage, if the section is not perpendicular to the wall, one gets the impression of two nuclei without a separating wall, as CHODAT (**3**) has shown in his fig. 660; but I found no case in which the wall was really lacking. Fig. 3 is an ovule with one of the large cells in mitosis, showing the 20 chromosomes of the diploid generation. The ovule is somewhat larger before the difference in staining reaction appears, and the difference in the size of the cells is also more striking (fig. 4).

The inner integument begins to develop at this time. Fig. 5 has both integuments and the sporogenous cell is in synapsis. Synapsis was not found in younger ovules, but apparently it continues for some time, as it was often found in much older ovules, judging by the development of the integument. CHODAT'S fig. 660, *c* (**3**), is similar to fig. 5, except that he shows the nucleus without other contents than the nucleolus. Only a few instances were found in which more than one cell showed both by size and staining reaction the sporogenous characteristics. Fig. 6 gives two sporogenous cells, the cell with the nucleus in synapsis being much the larger. In fig. 7 the cells are approximately the same size, but the section was cut so that one cell was unfortunately directly over the other. Here

the cell in synapsis is somewhat shorter and broader than the other. The walls of one cell are dotted in, but the walls of the other and both nuclei are drawn.

The mother cell divides in the usual manner (figs. 4, 8, 9). A full series was studied, but only a few drawings will be shown. In fig. 5 the synapsis stage is shown and in fig. 8 the spirem. The chromosomes are quite short and thick in fig. 9, and the haploid number (10) can be counted. The daughter cells sometimes differ slightly in size, but as a rule the difference is not marked (fig. 10). In fig. 11 the lower daughter cell has the spindle already formed for the second division, while the upper daughter cell has only formed the chromosomes, the nuclear membrane being still complete and very distinct. But in fig. 12 both daughter nuclei are in the early telophase of this division. In the upper cell one chromosome did not reach the pole and was left out of the megaspore nucleus. This condition was seen only a few times; and, as the upper megaspore always disintegrates in the material studied, it does not seem to be of any importance in the life-history of this plant. One example of the same condition was found in the first division. Here it might affect the life-history; for very often the second megaspore develops. If the nuclei continued to divide as usual, this might give an egg with one less than the usual number of chromosomes, in this case 9 instead of 10.

Figs. 13–15 show the different positions of the megaspores, a straight row in fig. 13, the two lower in a row and the two upper side by side in fig. 14, and approaching the tetrad form in fig. 15. CHODAT (**3**) gives in his fig. 661 a straight row of four megaspores and in fig. 662 a row of three cells; in both cases the lower megaspore has enlarged to produce the embryo sac.

EMBRYO SAC.—While in angiosperms it is probably true that the lowest of the four megaspores usually produces the embryo sac, the others disintegrating, cases showing that any of the four may function have been reported, and in some instances all four show sac tendencies. COULTER and CHAMBERLAIN (**4**, p. 84) give a summary of the literature on this subject. In *Parnassia* apparently the second or the third as frequently develops as the fourth (figs. 16–29), but no case was found in which the first developed. These

figures show that often two of the megaspores begin to develop, apparently either two of the lower three, second and fourth (figs. 16–18), second and third (fig. 17), third and fourth (figs. 22 and 24). In fig. 25 one of the two upper adjacent megaspores and the fourth one began to develop, but the upper one is in the best condition, the fourth one being less dark than the other two, but darker than the upper one. The epidermis is quite pale over this spore. Fig. 23 has the appearance of five megaspores, but one nucleus is quite small with apparently only one chromosome, and is probably the result of an abnormal division like that shown in fig. 12.

The epidermal layer of the nucellus begins very early to disintegrate. These cells nowhere had the usual appearance of disintegrating cells. As is well known, cells disintegrating under apparently similar conditions stain deeply and have a more or less crushed or squeezed appearance. But here they seem to grow paler, as if the cytoplasm within them were diminishing, and finally all contents disappear. Later the walls also are more or less completely absorbed. An attempt to show this is made in figs. 24, 26, 27. In fig. 24 the whole epidermal layer is pale almost to the base of the fourth megaspore; in figs. 26 and 27 the cells are disappearing from the upper part of the nucellus, leaving the megaspores lying next to the inner integument. The disintegration in this region continues until only the lower end of the sac is inclosed by nucellar tissue, the greater part of it being in contact with the integument and having no cells between it and the micropyle (figs. 30, 31, 33–36). CHODAT'S (**3**) figs. 661–666 show this disintegration of nucellar tissue. He says:

> Chez beaucoup de Gamopétales et ches quelques Dialypétales la mégaspore qui s'est développée dans un très petit nucelle dissont le sommet de celui-ci et fait saillie an dehors dans le micropyle.

The disorganization of this layer of cells may furnish food to the upper megaspores and thus give them a better chance to develop than they would otherwise have. On the other hand, it is altogether possible that this disintegration is due to the unusual activity of these megaspores.

Fig. 27 shows a two-nucleate sac that developed from the second megaspore; the third megaspore is quite large and as yet shows no

signs of disintegration. The fourth megaspore is fast disorganizing, being a darkly stained almost structureless mass. The first megaspore and the nucellar layer over the upper part of the sac show only traces of their former existence. An embryo sac developing from the fourth megaspore is shown in fig. 28. The nucleus is in mitosis for the first division, and the 10 chromosomes can be counted. The three upper megaspores are completely disorganized, and the nucellar cells near the micropyle are paler and with very little contents. The vacuole appears early in the two-nucleate sac (fig. 29). It is not common to find the second and the third megaspores persisting so long as they have here. The two upper nucellar cells have very little cytoplasm in them and stain much lighter than the others.

In fig. 30 an entire ovule at a little later stage is shown with less magnification. The nucellar layer has disappeared completely from around the upper part of the sac, leaving it in contact with the inner integument and an open micropyle all the way to the sac. The only part of the nucellus remaining is that below the lower.nucleus of the two-nucleate sac. It is interesting to note that SHREVE (**20**) has shown a similar figure for *Sarracenia*, all the nucellar tissue except that at the base having been destroyed. The loose, spongy tissue is already appearing in the chalazal end of the ovules. This becomes very conspicuous in older stages.

Figs. 31 and 32 show the second mitosis in the embryo sac. In one nucleus of each sac it is possible to count the 10 chromosomes. In the first the chromosomes have been formed in both nuclei, in the second only in the lower one; the upper one has the spirem very thick and short and probably shows the early stages of segmentation. In both ovules the nucellar layer has disappeared from the upper half of the sac. The spindles for the second division are at right angles to each other (fig. 33). This sac developed from the second megaspore, and in this case the third one has also begun to develop. Fig. 34 shows a four-nucleate sac with the chromosomes more or less completely segmented for the third division. The nucellar layer has disappeared from the upper two-thirds of the sac. The inner layer of cells of the integument is shown on one side of the sac in fig. 35. The sac nuclei are in the late anaphase of the third division. The upper spindle is almost perpendicular to the paper,

and so it is not easy to show it correctly. Each of these spindles shows the thickening of the spindle fibers in the center, characteristic of early wall formation, but further development of the walls does not take place, as is shown in fig. 36. The nucellar layer is represented by a more or less distinct line of stuff which can be traced to the perfect cells below the sac. The darker thicker mass near the micropyle is probably the remains of the megaspores.

The eight nuclei arrange themselves in the usual fashion (fig. 37). In this figure the egg lies just back of the synergids and only the lower part of it is shown in the drawing; and the polars are almost in contact. Here the large nucleoli characteristic of these nuclei are well shown, the nuclei having very little other stainable material in them. In this case practically all of this material is shown in the drawing, which was made not with a single focus, but by focusing in all parts of the nuclei. At any given focus one's first impression of the nucleus is an empty circle except for the very large nucleolus. The inner layer of cells of the integument is drawn on only one side of the sac. This layer has the appearance of the so-called tapetum or jacket layer formed in many of the Sympetalae, as well as in other forms, and is quite different in appearance from the adjacent cells. CHAMBERLAIN (1) has shown it in *Aster novae-angliae*. EICHINGER (6) says:

> Bei unserer *Parnassia* kann man füglich von einem Tapetum nicht sprechen, die innersten Zellen des Integuments unterscheiden sich nicht allzusehr von den andern.

But in my material the difference in shape and staining was striking.

Small vacuoles are already present in the synergids. One synergid shows the beginning of the indentation, *Leiste* of STRASBURGER (21), which in later stages gives a caplike appearance to the upper part of the synergid. It seems to be related to the cytoplasm of the sac, that is, it is always just where the cytoplasm of the sac reaches its highest point of contact with the synergid. It seems probable that, as the filiform apparatus develops (being of cellulose, it is somewhat stiff) and the synergids elongate, this upper stiffer part does not change shape so much as the lower part. A filiform apparatus is common in angiosperms, but it is not always so strikingly developed as here. In *Die Angiospermen und die Gymno-*

spermen (**22**), STRASBURGER shows (pl. 2, fig. 19) a filiform apparatus, but no notch in *Polygonum divaricatum*. COULTER and CHAMBERLAIN (**4**, p. 94) say that "such beak-like extensions of the sac and synergids are usually associated with narrow and long micropyles." But in *Parnassia* the micropyle is usually wide open and even all nucellar cells have disappeared from this region.

A similar filiform apparatus and notch are shown by STRASBURGER (**21**) in *Santalum*. This is shown quite clearly in spite of the very imperfect technique of that time. In *Santalum* the notch seems to be definitely related to the embryo sac wall, the upper part of the synergids protruding beyond the wall, and this indentation being just against the upper end of this broken wall. NAWASCHIN (**16**) shows in his fig. 9 a very deep notch in the synergids of *Helianthus annuus*. The synergids are pointed, but do not show the lines of the filiform apparatus in the upper part, although just below the notch the lines are quite distinct. This part of the figure is not described, and it may be that the upper part has the usual lines of the filiform apparatus, but they failed to appear in the plate. Here the notch seems definitely related to the cytoplasm of the sac, very much as it is in *Parnassia*. JUEL (**14**) shows the usual embryo sac in *Saxifraga granulata*, but does not describe a filiform apparatus. This stage he shows in a microphotograph which is quite indistinct in this region. Fig. 38 is slightly older; the filiform apparatus is beginning to develop in the synergids. The nucleus is above the vacuole in one and below it in the other synergid. Fig. 39 has an unusual development of the vacuoles in the synergids; here the polars are in contact. In fig. 40 the vacuoles are below the nuclei in both synergids, and the polars have fused, forming the primary endosperm nucleus. The filiform apparatus and notch are quite distinct by this time. Another view of a sac of about the same stage is shown in fig. 41. In this ovary many sacs were still in the four-nucleate condition.

The upper part of a mature sac is shown in fig. 42. The polars have already fused. In *Parnassia* they apparently always fuse immediately, as they are fused in all the mature sacs examined. The caplike filiform apparatus is always very conspicuous at this stage, and stains red with Congo red, which shows it to be cellulose. The

inner row of cells of the integument next to this part of the sac is disintegrating, the disorganization being more or less complete as far down as the last cell drawn, which seems to be still active, as both nucleus and cytoplasm have the usual staining reaction and structure of active cells. Fig. 43 is the other view of a similar sac, being cut at right angles to that of fig. 42; the other synergid is directly under the one drawn. Here the egg apparatus is farther up in the micropyle, and a few of the cells of the integument over the filiform cap have entirely disappeared. CHODAT (3) shows an embryo sac before and after fusion of the polars in his figs. 664 and 665, but does not show the filiform apparatus of the synergids. His fig. 677 suggests the possibility of its presence, but does not show it clearly. The pollen tube is just below it.

In many ovules the egg apparatus is entirely in the micropyle, a few of the cells of the integument being disorganized in most instances (fig. 44). The whole egg apparatus has the appearance of being squeezed into a space too small for it. The polars have fused. In fig. 45 the synergids lie one above the other in the micropyle, the egg being just at its entrance. These synergids show the notch and the filiform appearance quite distinctly. If the synergids are not entirely separated, they may have somewhat the appearance of pollen tubes; but it is always easy to distinguish them from the latter by the difference in staining reaction, and by the fact that the real tube structure is lacking. A diagram with less magnification (fig. 46) shows the whole upper portion of the ovule. Fig. 47 shows one synergid nucleus just at the entrance of the micropyle, some of the cytoplasm of this synergid being entirely outside of the ovule. In fig. 48 the entire egg apparatus is just at the entrance to the micropyle, with the polars in contact in the upper part of the sac. A few ovules were seen in which the whole of the egg apparatus was entirely outside of the micropyle. These figures with the synergids in the micropyle are very similar to the structures shown by CHODAT (3) in his figs. 675–676, which he calls pollen tubes.

POLLEN.—The anthers present the usual four-lobed appearance, with four sporogenous regions. A group of mother cells in more or less perfect synapsis is shown in fig. 49. After synapsis there is a thick spirem which segments into 10 chromosomes (fig. 50). The

telophase is shown in fig. 51. The chromosomes seem to remain distinct here (figs. 51 and 52) and could often be counted after the nuclear membrane was formed. Fig. 53 shows the metaphase of the homotypic division; the two spindles being almost at right angles, one nucleus is cut exactly at the plate and the other shows almost all of the spindle. The formation of the tetrad is shown in fig. 54. Different views of the microspores soon after their formation are shown in figs. 55 and 56. The nucleus divides at once to form the tube and generative nuclei (figs. 56–59). The wall apparently disappears early, as several gametophytes without a wall separating the two nuclei were found in these same anthers. The stages shown in figs. 55–59 come from the same anthers, all the anthers of this flower being in the same stage.

FERTILIZATION.—The pollen tube comes through the micropyle, which is usually open (figs. 30, 42, 43), curves around the tip of the synergid, and seems to empty into one of the synergids below the notch (fig. 60). In this sac the other synergid is quite dark, and the tube can be traced to this dark mass. Fertilization has already taken place, and there are two endosperm nuclei. In fig. 61 the same dark appearance of one synergid is found, and again the other synergid is unchanged. Fusion of the sex nuclei has already taken place; both the egg and the primary endosperm nucleus show much more chromatin than they do in the mature sac (fig. 43). Several pollen tubes were seen, all about the same stage. Only one more will be shown (fig. 62). In this the bending of the tube around the upper part of the synergid is not so clearly shown, as the section was not so fortunate in position as that in fig. 60, yet the tortuous course is quite evident. But especially clear is the emptying of the tube into one synergid. The contents of this synergid consist of a very darkly stained mass in which no structure can be distinguished except one nucleolus, which is quite clear because of its bright red color in the dark purplish mass. It is probably the nucleolus of the synergid nucleus. The other synergid is in the next section and is quite normal in every respect.

GUIGNARD (**11**) in *Nicotiana Tabacum* and *Datura laevis* reports the pollen tube passing into one synergid and discharging its contents there. JUEL (**14**) has described a similar passing of the

contents of the pollen tube into one synergid in *Saxifraga granulata*. CHODAT (**3**, p. 552) says:

> Lorsque le noyau fécondant est entré dans le sac on remarque qu'au moins l'une des synergids perd sa turgescence et se désorganise.

In his fig. 677 he shows a pollen tube which from the drawing might be either inside or outside of the synergid. In this mass are three nuclei, one evidently the synergid nucleus. Fig. 63 shows a sperm cell in each synergid. There seems to be a distinct layer of fine-grained cytoplasm about each of these nuclei. One synergid also has another somewhat irregular mass of nuclear stuff which is probably the tube nucleus. This sac was cut slantingly, so that the micropyle and filiform apparatus were in another section, but no trace of the pollen tube was found in this region. Another ovule in the same section had an embryo of five cells. But only a very few embryos were present in this ovary, and the other ovules did not show evidence of fertilization; so that probably only a few pollen grains had reached the stigma. These two dark synergids, each containing a sperm cell, might be interpreted as evidence of two pollen tubes in the same sac. But as there is no other trace of pollen tubes or other nuclei, and the egg and primary endosperm nucleus do not have the appearance of having been fertilized, it seems best to suppose that only one pollen tube has entered and that it burst just where the two synergids are in contact. In this way it would be possible for part of the contents to pass into one synergid and part into the other. .Both synergids are quite dark and show little trace of vacuoles, which are quite conspicuous in mature sacs.

NAWASCHIN (**16**) says that after the pollen tube passes the micropylar canal and the nucellus of the ovule, and its tip is in contact with the embryo sac, one of the synergids bursts and pours part of its contents into the micropyle. This forms a half-empty tube of this synergid, and the sudden diminution of pressure causes the pollen tube to burst and its contents are poured out next to this synergid into the sac. Then the sperm nuclei begin active movement toward the depression in the "Endospermanlage," and move from there to the female cells. In *Parnassia* it is very evident that the pollen tube passes around the tip of the synergid without either

synergid or pollen tube bursting, and that the tube empties into the synergid just below the notch. This process itself was not seen, as unfortunately all my material was too old to show this, even fertilization having already taken place in every case except one. But the pollen tubes themselves were unusually clear; they could often be traced through the entire micropyle to the point where they entered the synergid. CHODAT (3) shows the sex nuclei in various stages of fusion in his figs. 678–680.

EMBRYO.—One and two-celled embryos showed nothing unusual. The endosperm nucleus usually divides first; only one exception to this was seen (fig. 65). Here there is a five-celled embryo with the endosperm nucleus still undivided and somewhat amoeboid in shape, which is also unusual in *Parnassia*. One sac was seen with a two-celled embryo and two endosperm nuclei, one near the embryo and the other near the antipodals, and one synergid still perfect. Empty pollen tubes are often very persistent in *Parnassia*. It is not uncommon to find a pollen tube that can be seen through the greater part of the micropyle and with the curve at the entrance to the sac where it passes around the beak of the synergid, but with little trace of the synergids below this, when the embryo has 20 or more cells. In the second division in the embryo, the upper cell again divides in the same plane as the first division, while the lower cell divides at right angles (fig. 64). Fig. 65 shows the five-celled embryo. Not many embryos of this stage were seen, but this seems to be the usual arrangement of cells. Fig. 66 gives the next stage, where the upper cell had again divided in the longitudinal direction. In fig. 67 the dermatogen is differentiated, and a layer of endosperm about two cells in thickness extends entirely around the sac next to the wall; in the center are a few free nuclei. Soon the plerome and periblem are also differentiated, as can be seen from the end of the embryo in fig. 68. This entire embryo is outlined in fig. 69 and the plerome is dotted in. The two cotyledons are already formed, and the embryo now completely fills the upper two-thirds of the sac, except for a layer of endosperm about two cells thick around it. The lower third of the sac is filled with endosperm. CHODAT (3) in his fig. 756 shows embryos from the two-celled stage to the differentiation of the dermatogen; his figures 756–775 are similar to my figures 75 and 81.

Saxifraga

Several species of *Saxifraga*, growing in the Botanical Garden in Bonn, were examined, to be sure that the usual form of this genus was known. The same methods of fixing and staining were used for *Saxifraga*, *Heuchera*, and *Drosera* as had been employed with *Parnassia*.

JUEL (**14**) has given a description of *Saxifraga granulata* which agrees in all the stages shown with the stages here figured; and I have examined *S. ligulata*, *S. sponhemica*, *S. cordifolia*, and *S. crassifolia*, which seem to be so similar that the same figures could be used for each. Not much work was done with the reduction division; but the reduced number of chromosomes in *S. sponhemica* is about 15. JUEL (**14**) found this to be about 30 in *S. granulata*. These two numbers are rather suggestive, especially since GATES'S (**10**) investigation of *Oenothera gigas* and STRASBURGER'S (**23**) discussion of this question.

Nothing unusual was seen in the pollen development of *Saxifraga*. The pollen grains are small and with smooth, rather thin walls. It might be of interest to note that in many of the flowers of *S. cordifolia* some of the anthers contained pollen at least twice the usual diameter, and in some cases as much as four times. In one flower this large pollen was found in every other anther, the younger set of stamens all being affected. But not all flowers produced this large pollen, and it was usually irregular in occurrence when present. As all the later flowers were blighted, turning black before the inflorescence was out of the bud, this peculiarity of the pollen was probably due to a fungus; but this was not investigated.

Two young ovules of *S. sponhemica* from the same ovary are shown. Fig. 71 shows the archesporial cell, and fig. 72 a later stage in which there is one sporogenous cell and the primary parietal cell has divided. The mother cell stage is shown in fig. 73, with two parietal cells. In fig. 74 there are three sporogenous cells, only one of which has reached the mother cell stage; a later stage is shown in fig. 75. There are three parietal cells above the mother cell in fig. 76. The whole of this ovule is shown in fig. 79. In *Saxifraga*, so far as examined, the megaspores are always in a row (fig. 78), and the fourth one develops the embryo sac. Not so much material

was examined as in *Parnassia*, but enough to be sure that the development of the other megaspores, if it takes place at all, is not common. The position of the megaspores in the nucellus is shown in fig. 79. Their great depth in the nucellar tissue is in striking contrast to *Parnassia*, where they are immediately below the epidermis, which is disorganizing at this stage.

Fig. 80 outlines an entire ovule with a two-nucleate embryo sac. There are no air spaces, the whole ovule being very compact and much more massive than that of *Parnassia*. The egg apparatus of a mature sac is shown in fig. 81. The synergids have a well developed filiform apparatus and a notch almost if not quite as deep as that in *Parnassia*. A diagram of this entire sac is shown in fig. 82. Two of the antipodals had disappeared. The polars have already fused and the primary endosperm nucleus is near the base of the sac. This seems to be its usual position in *Saxifraga*, at least in the examples I studied. JUEL (**14**) shows it near the middle or toward the antipodal region in *S. granulata* at fertilization. Fig. 83 is a young embryo which has just been differentiated into long suspensor and embryo proper. Two endosperm nuclei are shown.

Heuchera brixoides

This species corresponds so closely with *Saxifraga* that only three figures will be shown. There is usually one mother cell in *Heuchera*. One ovule with two mother cells (fig. 84) is shown, a later stage (fig. 85) with a large amount of parietal tissue, and a mature embryo sac (fig. 86). The placentae of *Heuchera* are like those of *Parnassia*, and quite unlike those of *Saxifraga*.

Drosera rotundifolia

This material was collected near Bonn. ROSENBERG (**19**) has worked out a very interesting chromosome relationship of *D. rotundifolia*, *D. longifolia*, and *D. intermedia*. In his early paper (**18**) he does not figure certain stages which I need for comparison, only quoting from C. A. PETERS (**17**, p. 275):

> Each nucellus produces a sporogenous layer of four cells, but no tapetum. Three cells of the sporogenous tissue soon disintegrate, leaving the fourth, which is the mother cell of the embryo sac and which undergoes subsequent cell division as is usual in angiosperms.

I shall give a few figures, therefore, in order to compare them with *Parnassia* and *Saxifraga*.

The mother cell in synapsis is shown in fig. 87. It will be seen that like *Parnassia* and *Saxifraga* no parietal cells were produced by the archesporium. This is the commonest condition in *Drosera*. But frequently a parietal cell is cut off which divides, as is shown in fig. 88, giving a row of two parietal cells above the mother cell. Occasionally more than one sporogenous cell is produced (fig. 89); but I saw no evidence that more than one embryo sac was produced, or even that more than one cell reached the mother cell stage. The usual row of four megaspores resulting from these two positions of the mother cell are shown in figs. 90 and 91. In some instances the megaspores are not in a row, as ROSENBERG (**19**) has shown in his text fig. 27, *B*, which is similar to fig. 25 in *Parnassia*. So far as examined, only the fourth megaspore develops in *Drosera*. Not so much material was cut as for *Parnassia*, but it is at least certain that the development of the other spores is not common as it is in *Parnassia*.

In *Drosera*, even in the mother cell stage (fig. 87), air spaces begin to develop in the chalazal region of the ovule. These spaces are quite large by the time the embryo sac has reached the two-nucleate stage (fig. 92), and in the mature ovule they are at least as strikingly developed as in *Parnassia*. The embryo sac occupies only the upper third of the nucellus even at maturity, quite in contrast to *Parnassia* and *Saxifraga*. The nucellus also begins to show its peculiar enlargement of cells. The outer layer of nucellar cells, except those directly over the embryo sac, increase enormously in size without increase of cytoplasm or size of nucleus; the latter lies next to the inner side of the cell. This enlargement of the nucellar cells, as well as the air spaces, reduces the specific gravity of the seed. DIELS (**5**) says:

> They are by their constitution capable of floating. HOLZNER states that the seeds of *D. rotundifolia* at a temperature of about 20° are capable of floating for about a month.

In fig. 93 the third division in the sac is shown and enough of the nucellus to show the differentiation in it. In one nucleus the 10 chromosomes may be counted.

The mature sac (fig. 94) has the usual appearance. The synergids have a well developed filiform apparatus and notch. The former is somewhat more dome-shaped than in *Parnassia*, where it is pointed. The synergids are also rather long, reaching almost as far as the lower edge of the egg. The polar nuclei have already fused. Fertilization apparently takes place as in *Parnassia*. The pollen tube passes around the filiform apparatus and seems to enter one synergid (fig. 95). Here probably the fusion of the sex nuclei has already taken place, as only one nucleus can be distinguished in the lower part of the dark synergid and probably another in the still darker mass higher up. Fig. 96 is clearer in this respect. A small bit of the pollen tube can be seen in contact with the filiform apparatus. This synergid is somewhat darkly stained, but still all structures are distinct, the notch and two nuclei; these are the synergid nucleus and the tube nucleus from the pollen tube. The other synergid is very pale and all the lower part has disappeared. The fertilized egg has not yet divided, but the primary endosperm nucleus is in mitosis; the spindle fibers are forming. So far as examined, this nucleus always divides before the fertilized egg in *Drosera*. Many cases were seen with two endosperm nuclei and the egg still undivided.

Discussion

Three other genera of the Saxifragaceae have been more or less completely worked out. EICHINGER (**7**) figures an ovule of *Chrysosplenium* with mature embryo sac that has three layers of nucellar tissue above the sac. In *Astilbe* WEBB (**25**) reports several archesporial cells and one or even two or three megaspore mother cells beginning to divide. The embryo sac is deep in the nucellar tissue, but no filiform apparatus is shown. The embryo has a suspensor of several cells. FISCHER (**9**) in *Ribes aureum* shows ovule development similar to that of *Saxifraga*, except that the filiform apparatus is not shown. TISCHLER (**24**) in a mature embryo sac of *Ribes sanguineum* shows pointed synergids but no filiform apparatus or notch. These cases may indicate that these three genera do not have the filiform apparatus and notch. But it is also possible that the material studied was not at the right age to show these best, or was not cut to the best advantage for these particular structures.

In a recent number of *Das Pflanzenreich* on Droseraceae, DIELS (**5**) says, in discussing relationships:

Die mehrfach den Droseraceen angeschlossene Gattung *Parnassia* wird neuerdings nach dem Vorgang von ADAMSON, ENDLICHER, LINDLEY, und PAYER, allgemein ausgeschlossen nachdem DRUDE in seine gründlichen Eröterung der Frage (Linnaea **39**:293. 1875) auf die gewichtigen Bedenken practischer Natur' hingewiesen hatte, die einer Überführung von *Parnassia* zu den Droseraceen im Wege stehen.

ENGLER (**8**), in a note in connection with the Sarraceniaceae, concludes with these words:

Die Droseraceae nähere sich dadurch in diagrammatische Beziehung manchen Saxifragaceae, von denen *Parnassia* auch allgemein den Droseraceae zugerechnet wurde.

The following is a rather free translation of EICHINGER'S (**6**) summary of the characters which differentiate *Parnassia* from Droseraceae:

1. *Germination.*—*Parnassia* shows normal germination; cotyledons do not function as an absorbing apparatus. The Droseraceae have no primary root; cotyledons have more or less the function of an absorbing apparatus.

2. *Leaf structure.*—The nervature is different. *Parnassia* possesses a typical leaf structure, in the epidermis tannin; the Droseraceae have no typical assimilation tissue and often chlorophyll in the epidermis, and always more or less modified glands.

3. *Flowers.*—All species of *Parnassia* have staminodia; the Droseraceae have not.

4. *Befruchtungsvorgang* (apparently pollination).—It is apparently similar in species of *Parnassia*, has no analogy to the Droseraceae, but has to *Saxifraga*.

5. *Androecium.*—*Parnassia* possesses small simple pollen grains; all of the Droseraceae have tetrads.

6. *Gynaecium.*—*Parnassia* has stalked placentae, a very striking conductive tissue, the nucellus is small-celled and soon vanishes, the embryo is well formed and fills the almost endospermless seed. *Drosera* at least has flat placentae without conductive tissue, characteristically differentiated nucellus, and all of the Droseraceae have small, round, imperfect embryos and much endosperm.

HALLIER (**12**) says:

Under the Saxifragaceae the genus *Parnassia* takes an isolated place. According to its peculiar habit, its low rosette of long-petioled oval leaves, its one-flowered, long, almost leafless flower-stalk, and the lack of hairs, it evidently belongs not to the Saxifragaceae, but in ENGLER'S order Sarraceniales, which, through the frequent appearance of oval, long-petioled, fleshy leaf blades,

long, one or few-flowered peduncle, fleshy, white, oval floral leaves, and its great predilection for wet or moist places, reveals its descent from the relatives of the Nymphaeaceae, and it manifestly has nothing to do with the Saxifragaceae, which are nearly related to the Rosaceae. Apart from the peculiar staminodia, which are evidently morphologically equivalent to the staminodia of many Nymphaeaceae, the fibers (*Fäden*) in the *Rafflesia*, flower, and the corona of *Passiflora*, *Parnassia* fits closely to *Drosera* through its leaf-rosette, its long, almost leafless shaft, the calyx, the five beautiful white petals, the sessile stigmas, the numerous parietal ovules, the method of capsule opening, the small oblong seed, rich in endosperm, and moist habitat. Through its four-leaved (four-carpellate) seed coat it approaches *Nepenthes* also.

A summary of the parts studied by way of comparison may be helpful.

1. The ovule of *Parnassia* and *Drosera* are of the same shape, and both have large air spaces developed. That of *Saxifraga* is very compact and much thicker, and with thicker integuments.

2. In *Parnassia* the archesporium of the ovules is hypodermal and forms no new cells above it. *Drosera* usually develops in the same way, but sometimes there is a single layer of cells between the mother cell and the epidermis. All the Saxifragaceae studied form the archesporium in the same way, but by the time the mother cell stage is reached there are several layers of cells above it.

3. In *Parnassia* the embryo sac comes to lie next to the integument except the very basal portion, all the nucellar cells above and at the side having been destroyed. In *Drosera* the nucellar cells above the sac have a squeezed appearance and are occasionally destroyed completely. At the side and below the sac the layer of cells next the epidermis enlarge very greatly, giving the nucellus of *Drosera* a very peculiar appearance. This may be only another means of decreasing the specific gravity of the seed. The sac of the Saxifragaceae has several layers of nucellar cells above it.

4. All three genera have an enormous development of the filiform apparatus of the synergids, and the notch is also strikingly developed. The filiform apparatus is pointed in *Parnassia* and Saxifragaceae, and less pointed or more dome-shaped in *Drosera*.

5. The primary endosperm nucleus in *Parnassia* and in *Drosera* is immediately below the egg. In *Saxifraga* it is almost in contact with the antipodals, and in *Heuchera* it is far below the egg.

6. The haploid chromosome number in *Parnassia* and in *Drosera rotundifolia* is 10, in *Saxifraga sponhemica* about 15, and in *S. granulata* about 30.

7. In *Parnassia* and *S. granulata* the pollen tube empties into one synergid, and apparently the same is true in *Drosera*.

With reference to the systematic position, EICHINGER (**6**) says that the joining of *Parnassia* to the Droseraceae would completely destroy the unity of this family. Its principal characteristic would be lost. The failure of a primary root, the defective differentiation of the assimilation tissue, the stipular structures, which recall the intra-ovarian scales of many water plants, the numerous secretion glands, the common appearance of cleistogamous and autogamous flowers, the high capability for regeneration, and the appearance of vegetative buds are most important. In *Parnassia* no such relation to water plants is found. If one looks for a suitable place in the system for *Parnassia*, one must admit that it had better remain with the Saxifragaceae. This family has at present so little unity that *Parnassia* makes no break in its systematic characteristics. In discussing the same question, HALLIER (**13**) says: according to the pronounced monocotyledonous type of venation of the sepals and petals, it seems to me to stand not very far from the point of departure of the monocotyledons and as the representative of a separate family, the Parnassiaceae, to belong near the Ranunculaceae, Nymphaeaceae, Droseraceae, and Sarraceniaceae. From the Saxifragaceae, in which ENGLER (**18**) has placed it, it is differentiated by the harp-shaped branching of the veins in the sepals, the large, long *Podophyllum* and *Sarracenia*-like anthers, and the ovule, which has a slender nucellus, as in other relatives of the Saxifragaceae.

After working over my material, I am of the opinion that *Parnassia* is much more closely related to the Droseraceae than to the Saxifragaceae, and that it should at least be put in the same order with the Droseraceae. For as shown above, *Drosera* and *Parnassia* are quite alike in their ovules and in embryo sac development, except as to the nucellus, in which neither is like *Saxifraga*. They differ also in that *Parnassia* has stalked placentae, while *Drosera* has not. *Drosera* has pollen grains in tetrads and *Parnassia*

has them separate. But in neither of these characters does *Parnassia* agree with *Saxifraga*, whose placentae are still more dissimilar and whose pollen grains are perfectly smooth.

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EXPLANATION OF PLATES XIV–XVII

All figures except the diagram in fig. 70 were drawn with the aid of the camera lucida; Spencer ocular no. 4 and 4 mm. objective were used for figs. 5, 30, 45, 46, 47, 48, 67, 68, 77, 79, 80, and 92; ocular no. 4 and 16 mm. objective were used for fig. 69; all others were drawn with ocular no. 4, 1.5 mm. (oil) objective.

The abbreviations used are as follows: *e*, egg; *m*, megaspore; ♂, male nucleus; *p*, pollen tube; *s*, synergid; *t*, tube nucleus.

Parnassia palustris

FIG. 1.—Young ovule with three large hypodermal cells; two shown in the drawing; the third is just back of these two.

FIG. 2.—A somewhat older ovule with four large cells in a row, evidently derived from a single hypodermal cell by two successive divisions.

FIG. 3.—A different arrangement of the large group of cells, one cell in mitosis, showing 20 chromosomes; from the same ovary as fig. 5.

FIG. 4.—Sporogenous cell differentiated as shown by size and stain; the inner integument is beginning to develop.

FIG. 5.—Synapsis and beginning of outer integument.

FIG. 6.—Two sporogenous cells; the larger one already in synapsis.

FIG. 7.—Two sporogenous cells of approximately the same size; the two cells were in the same section, one lying above the other; the larger cell has the nucleus in synapsis, the other one in an earlier stage.

FIG. 8.—After recovering from synapsis; spirem still very long.

FIG. 9.—Ten short chromosomes; the double character can be clearly seen in several.

FIG. 10.—The two daughter cells with chromosomes formed for the second division.

FIG. 11.—The micropylar daughter cell in same stage as fig. 10; the chalazal daughter cell has nucleus with spindle.

FIG. 12.—Both daughter cells in the telophase stage; in the micropylar cell one chromosome failed to reach the pole and so is omitted from the megaspore nucleus.

FIG. 13.—Four megaspores, apparently all increased in size but the first disintegrating, and the second and fourth larger than the third.

FIG. 14.—A different arrangement of the four megaspores, probably occurring more often than that shown in fig. 13.

FIG. 15.—Approaches still more nearly the usual tetrad arrangement.

FIGS. 16–22.—The variations in the early stages of the megaspores.

FIG. 23.—Apparently five megaspores; one nucleus is very small and seems to have only one chromosome, probably resulting from an abnormal division like that in fig. 12.

FIG. 24.—Third and fourth megaspores developing; the nucellar cells surrounding these are already showing signs of disintegration, and only the three at the base are still normal in appearance.

FIG. 25.—In this case also the epidermal cells are becoming pale, especially over the upper vigorous megaspore, which appears to be more active than the fourth.

FIG. 26.—The third megaspore forming the embryo sac and in mitosis for the first division; the epidermal layer partly disorganized, leaving the sac in contact with the inner integument and an open micropyle.

FIG. 27.—Two-celled sac formed from second megaspore; the third megaspore also developing; the epidermal layer still further disorganized.

FIG. 28.—Embryo sac formed from the fourth megaspore; first division showing 10 chromosomes, the other megaspores represented by a formless mass above; epidermal layer still perfect; integuments well advanced.

FIG. 29.—All the epidermal layer, especially the two upper cells of the nucellus, lighter than the adjacent integument cells; two-celled sac from the fourth megaspore; the second and third megaspores have persisted longer than usual.

FIG. 30.—The entire ovule with two-celled embryo sac; ovule with loose spongy tissue at base; nucellus entirely lacking over greater part of sac.

FIG. 31.—Two-celled sac with nuclei in mitosis for the second division; the 10 chromosomes may be seen in the upper nucleus; the upper half of the sac is in contact with the integument, the nucellus having entirely disappeared from this region.

FIG. 32.—Similar to fig. 31, but the lower nucleus somewhat in advance of the upper; in the lower the chromosomes are short and thick, while in the upper the spirem is segmenting.

FIG. 33.—Spindles for the second mitosis in the embryo sac; this sac developed from the second megaspore; the third megaspore also developing.

FIG. 34.—The four-nucleate embryo sac with the spirems more or less completely segmented for the third division.

FIG. 35.—Spindles for the third division in the embryo sac; in the upper part of the sac one spindle is almost at right angles to the paper.

FIG. 36.—Eight-nucleate sac soon after the third division.

FIG. 37.—Embryo sac soon after the organization of the egg apparatus, the egg being just under the synergids; only the lower part of it with part of its nucleus can be seen; polars not yet in contact.

FIG. 38.—Upper end of sac, slightly older than in preceding figure; one synergid has vacuoles above the nucleus, the other has them below it; the so-called filiform apparatus beginning to be differentiated near the tip of the synergids.

FIG. 39.—From older sac; the synergids have unusually large vacuoles, both above the nuclei; polars are in contact.

FIG. 40.—The polar nuclei have fused; vacuoles below the nuclei in the synergids; the filiform apparatus well developed and forming a caplike structure.

FIG. 41.—This sac was cut at right angles to the one above, showing the whole of the egg, but only one synergid; this ovary still contained four-celled sacs.

FIG. 42.—Upper end of mature embryo sac; the unusual development of the filiform apparatus clearly shown; the inner layer of cells of the integument disintegrating.

FIG. 43.—Same stage as the preceding, but with the egg apparatus still farther up in the micropylar region; some of the cells of the integument entirely disorganized.

FIG. 44.—The entire egg apparatus in the micropyle, the adjacent cells of the integument having disappeared and the egg apparatus having a squeezed appearance.

FIG. 45.—The upper part of an ovule outlined; the egg apparatus in the micropyle, one synergid lying above the other.

FIG. 46.—Egg apparatus in the micropyle, but the synergids so pressed together that it is not possible to differentiate them.

FIG. 47.—A diagram of the upper part of an ovule; one synergid has the upper end entirely out of the ovule, its lower end overlapping slightly the upper part of the other synergid.

FIG. 48.—The entire egg apparatus just at the entrance of the micropyle, giving the appearance of a pollen tube; the polar nuclei are in contact but have not yet fused.

FIG. 49.—A few pollen mother cells; in two of these synapsis is perfect, in the others almost so.

FIG. 50.—The 10 chromosomes may be counted in this pollen mother cell.

FIG. 51.—Telophase of the first division.

FIG. 52.—Telophase of the first division in which the 10 chromosomes are still distinct.

FIG. 53.—Metaphase of the second division, one nucleus showing the spindle and the other being cut parallel with the nuclear plate and showing the 10 chromosomes.

FIG. 54.—The tetrad with a few spindle fibers still present.

FIGS. 55–59.—Stages in the division of the pollen grain into vegetative and generative cells; in fig. 57 the 10 chromosomes are shown.

FIG. 60.—Fertilization: the pollen tube curved around the upper part of the synergid, which is quite dark; apparently the sperm has already fused with the egg; the endosperm of this sac is two-nucleate.

FIG. 61.—The male nuclei have already fused with the egg and the primary endosperm nucleus; the dark mass underneath the synergid and outlined through it is the other synergid and some material from the pollen tube.

FIG. 62.—Pollen tube entering one synergid; the other synergid is just back of this one; fertilization has already taken place; the endosperm nucleus has divided, the other endosperm nucleus being near the antipodals.

FIG. 63.—The upper end of an embryo sac; in each synergid is a synergid nucleus and another smaller dense nucleus (a male nucleus with fine-grained cytoplasm around it); one synergid has a third nuclear mass, the tube nucleus.

FIG. 64.—Mitosis in both nuclei of a two-celled embryo.

FIG. 65.—Five-celled embryo with endosperm nucleus still undivided.

FIG. 66.—An older embryo with traces of a synergid and showing one endosperm nucleus.

FIG. 67.—Older embryo with dermatogen layer differentiated; the endosperm forms a layer about two cells in thickness all around the sac with a few free nuclei in the interior, especially around the lower end of the embryo.

FIG. 68.—The basal part of older embryo, showing dermatogen, plerome, and periblem.

FIG. 69.—The same embryo outlined; a typical straight dicotyledonous embryo which fills about two-thirds of the sac except for the layer of endosperm about two cells in thickness; the other third of the sac is filled with endosperm.

FIG. 70.—A diagram of an abnormal flower; one anther has developed on a staminodium, two are normal, the others, more or less imperfect, are on the carpels, which are not so completely united as usual.

Saxifraga

FIG. 71.—*S. sponhemica:* outer half of young ovule showing archesporial cell.

FIG. 72.—Same: the archesporial cell has divided.

FIG. 73.—*S. crassifolia:* one mother cell.

FIG. 74.—Same: one mother cell, but two other cells are quite large and stain like sporogenous cells.

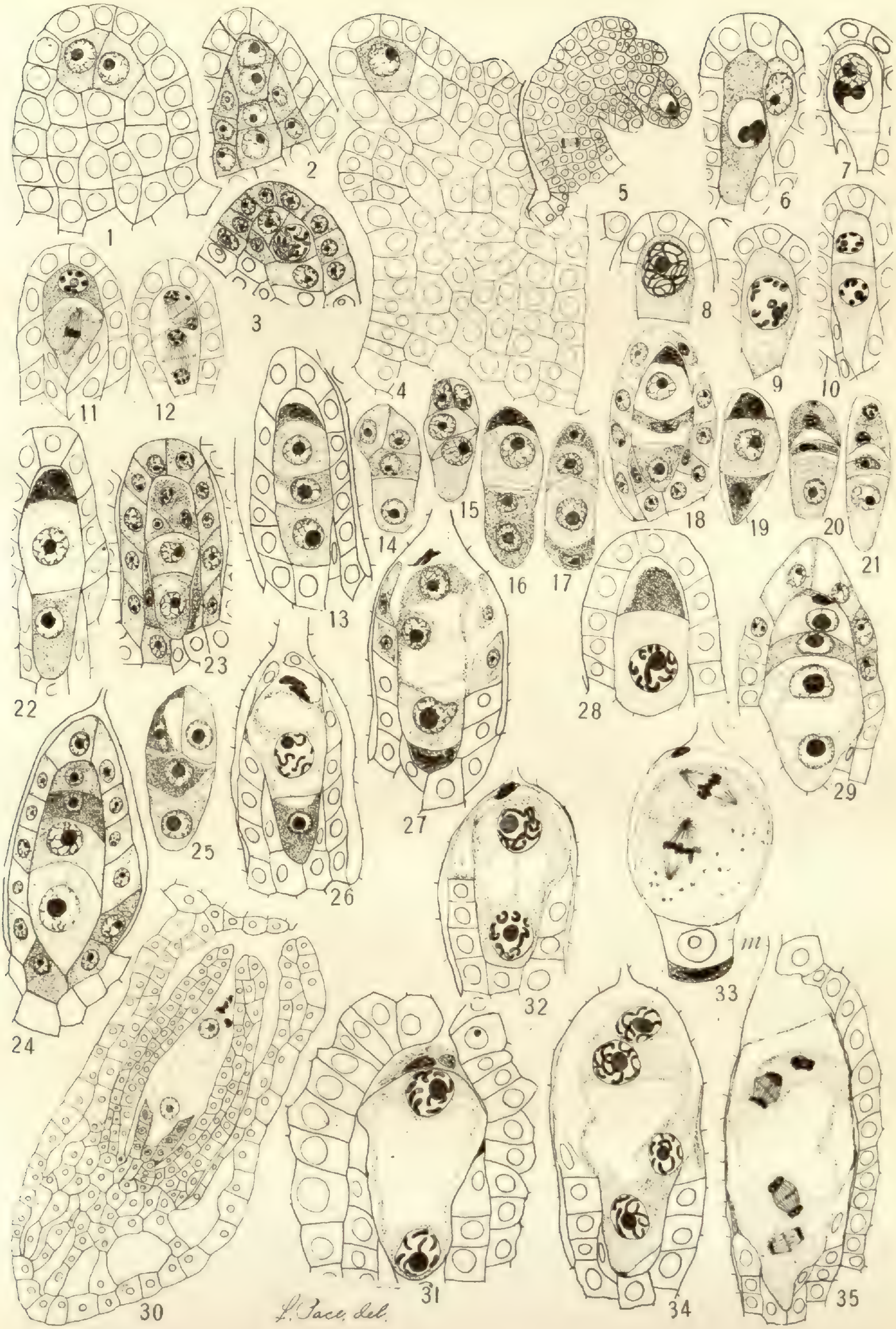
FIG. 75.—*S. cordifolia:* one sporogenous cell.

FIG. 76.—*S. crassifolia:* mother cell with three parietal cells.

FIG. 77.—Same: entire ovule with less magnification.

FIG. 78.—*S. ligulata:* megaspores; the lower are enlarging for the embryo sac.

FIG. 79.—Same: some megaspores showing nucellar tissue above.



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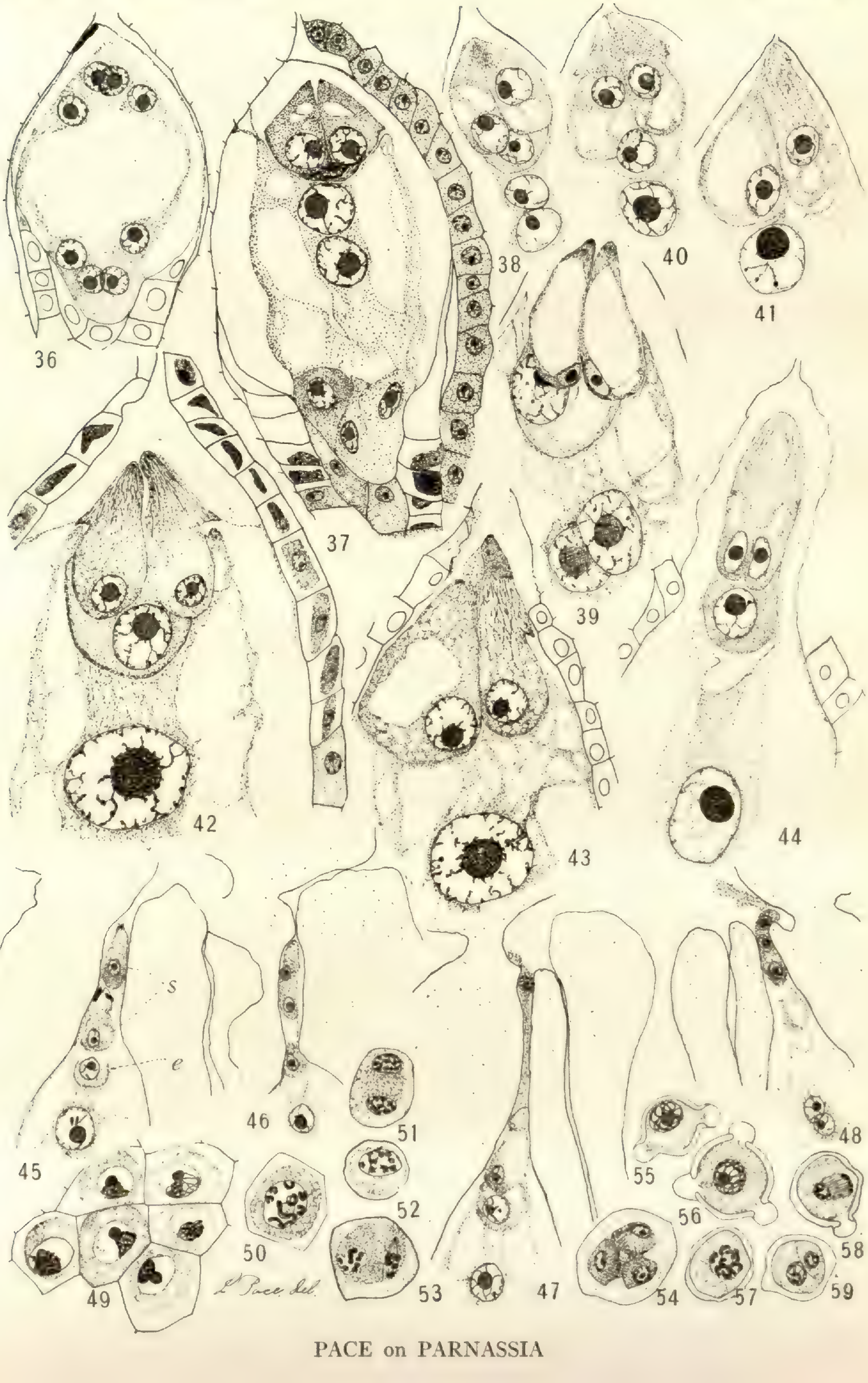

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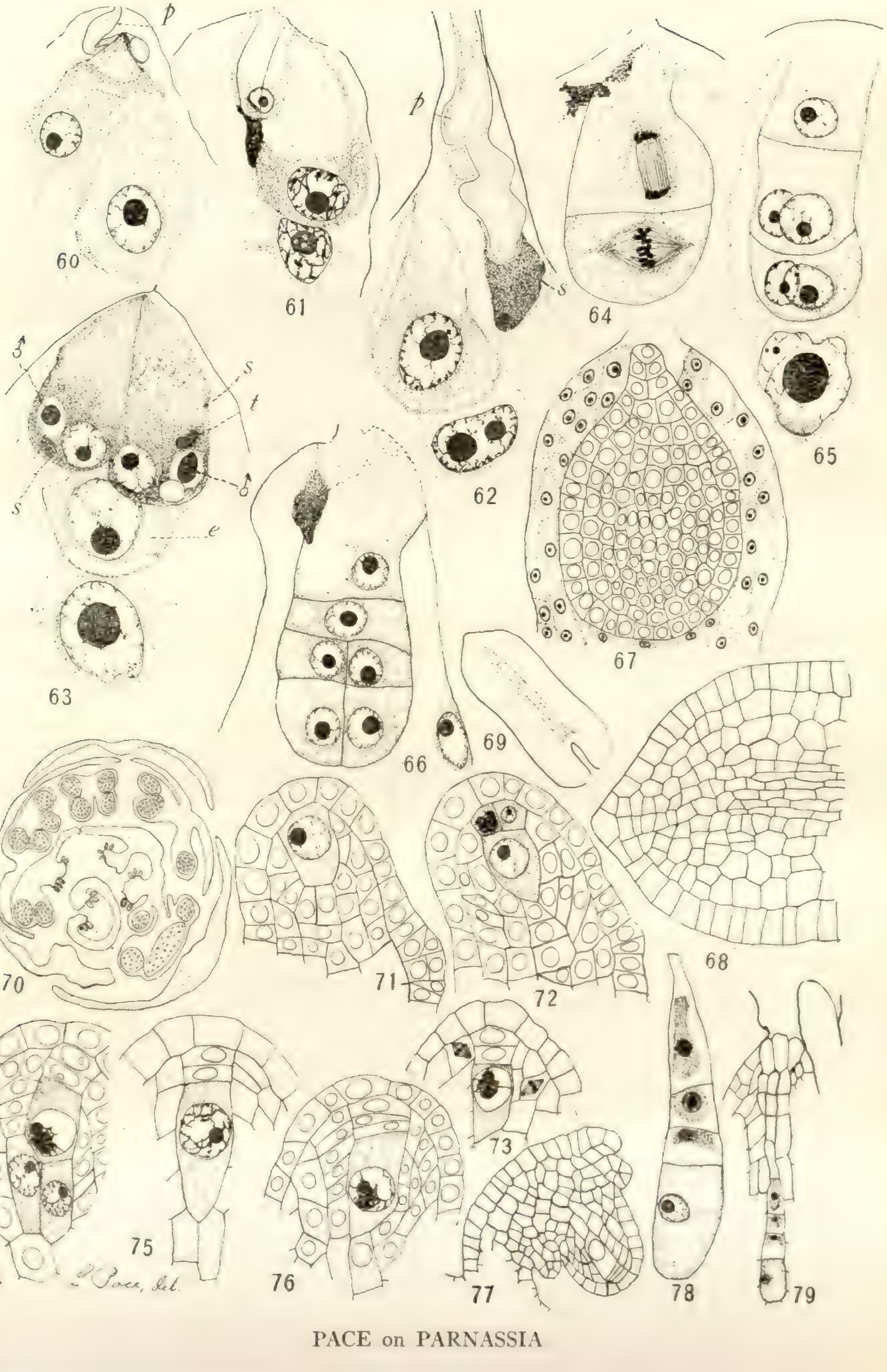

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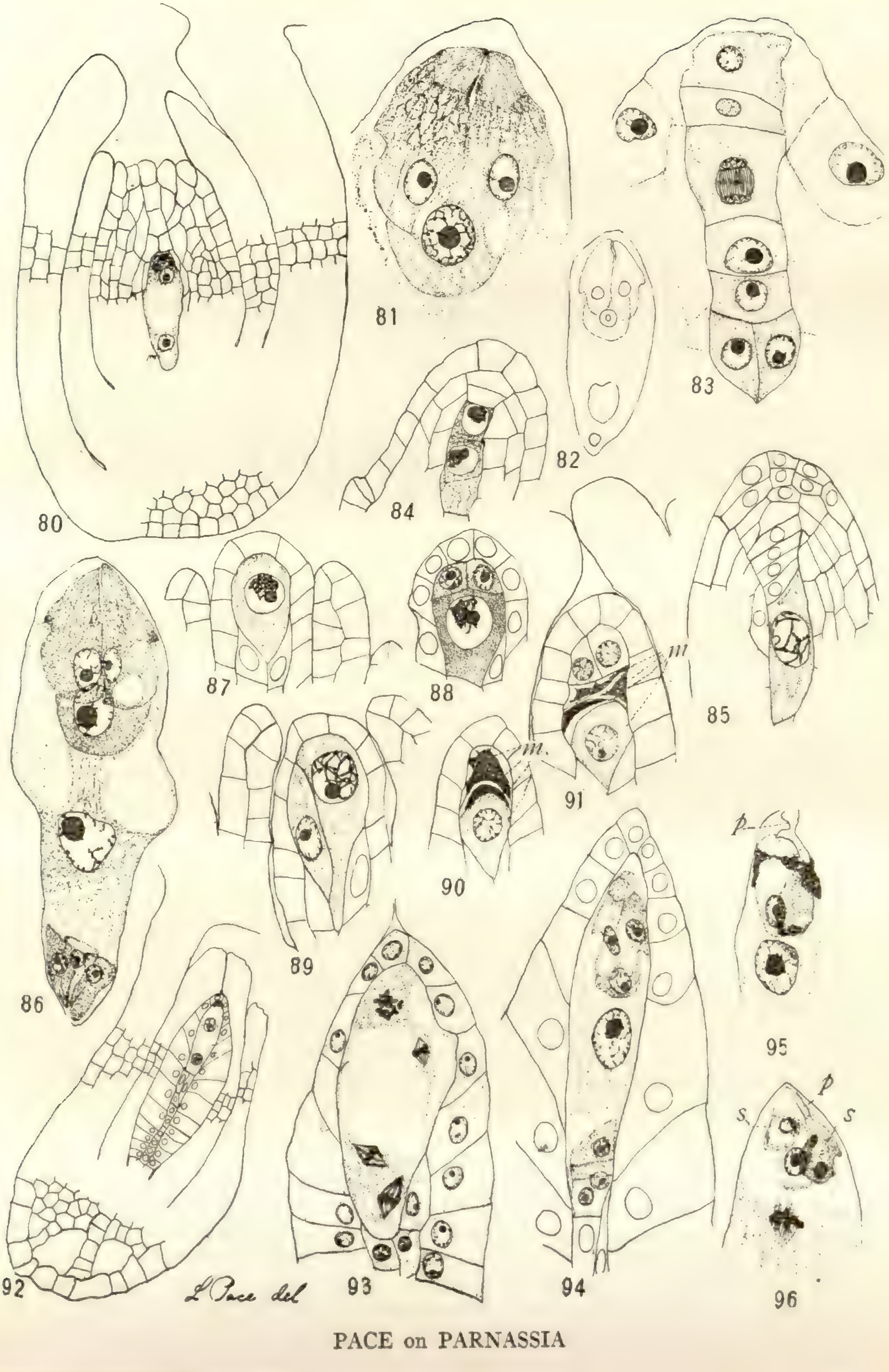


PACE on PARNASSIA

FIG. 80.—Same: a diagram of an entire ovule with two-nucleate sac; very compact tissue throughout the entire ovule.

FIG. 81.—*S. cordifolia:* egg apparatus.

FIG. 82.—Diagram of the same sac, showing one antipodal and the polars already fused near the base of the sac.

FIG. 83.—*S. crassifolia:* embryo and two endosperm nuclei.

Heuchera brixoides

FIG. 84.—Part of ovule showing two mother cells which are not exactly parallel and overlap slightly.

FIG. 85.—Mother cell after synapsis and deep in nucellar tissue.

FIG. 86.—Mature embryo sac; filiform apparatus and notch well developed in the synergids.

Drosera rotundifolia

FIG. 87.—Mother cell.

FIG. 88.—Mother cell with two hypodermal cells above.

FIG. 89.—At least two sporogenous cells, one of which has passed the synapsis stage.

FIG. 90.—Megaspores developed from a mother cell like that in fig. 87; the fourth megaspore has begun to develop the embryo sac, the other three are almost completely disorganized.

FIG. 91.—Similar megaspores, but developed from a mother cell like that in fig. 88.

FIG. 92.—An ovule with two-nucleate embryo sac; large air spaces and much spongy tissue in the lower part of the ovule; nucellar tissue with very small cells in center and very large ones next to the integument except just over the sac.

FIG. 93.—The third division in the embryo sac; in the upper nucleus the 10 chromosomes may be counted; the small nucellar cells just over the sac and the very large ones toward the base and the small ones in the center of the nucellus below the sac give the *Drosera* nucellus a very unusual appearance.

FIG. 94.—Mature embryo sac; the synergids have a well developed notch and a somewhat dome-shaped filiform apparatus; the polars have already fused.

FIG. 95.—An embryo sac with pollen tube passing around the filiform apparatus and apparently emptying into the synergid; probably the sex nuclei have already fused, but the mass is so indistinct one cannot be sure of the contents of the synergid region.

FIG. 96.—One synergid shows still a trace of the nucleus and the filiform apparatus; the other synergid shows the notch and above a bit of the pollen tube; in the lower part are two nuclei, probably the synergid nucleus and tube nucleus; the sex nuclei have fused and the endosperm nucleus is in mitosis.

DEVELOPMENT OF THE MICROSPORANGIA AND MICROSPORES OF ABUTILON THEOPHRASTI

V. LANTIS

(WITH TWELVE FIGURES)

The material used in this study was collected during September and October 1910. While many killing and fixing fluids were tried, Flemming's weaker solution proved the most satisfactory and was therefore the most generally used.

Because of the excessive development of sclerenchymatous tissue in this form, much difficulty was first experienced in sectioning. This was obviated, however, by infiltrating and imbedding in JOHNSTON'S paraffin-asphalt-rubber mixture (**11, 16**), which consists of 99 parts of paraffin (desired grade) in which has been melted enough asphalt (mineral rubber) to give the paraffin an amber color, and one part of crude india rubber. This method, in that it has proved so satisfactory, deserves a more general use among botanists. Many stains were tried, but Heidenheim's iron-alum hematoxylin, with orange G as a contrast stain, gave the best results.

The stamens of *Abutilon Theophrasti* Medic. are epipetalous, monadalphous, and branching. Occasionally the branches of the filaments are so short that the two anthers set back to back, and the two might be taken for one anther in a hasty examination. In longitudinal section the anthers are more or less crescentic in form, while a cross-section shows them to be two-rowed (fig. 5). In this respect it is very much like *Althaea rosea* Cav. (**2, 4**) and *Tilia ulmifolia* (**7**). It is not at all uncommon to see one lobe much longer and more crescentic than the other. The filament is attached to the middle of the inner side of the crescent-shaped anther. Dehiscence takes place by means of one longitudinal fissure.

There are two crescent-shaped microsporangia in each anther, one in each of the two lobes. With respect to the number of

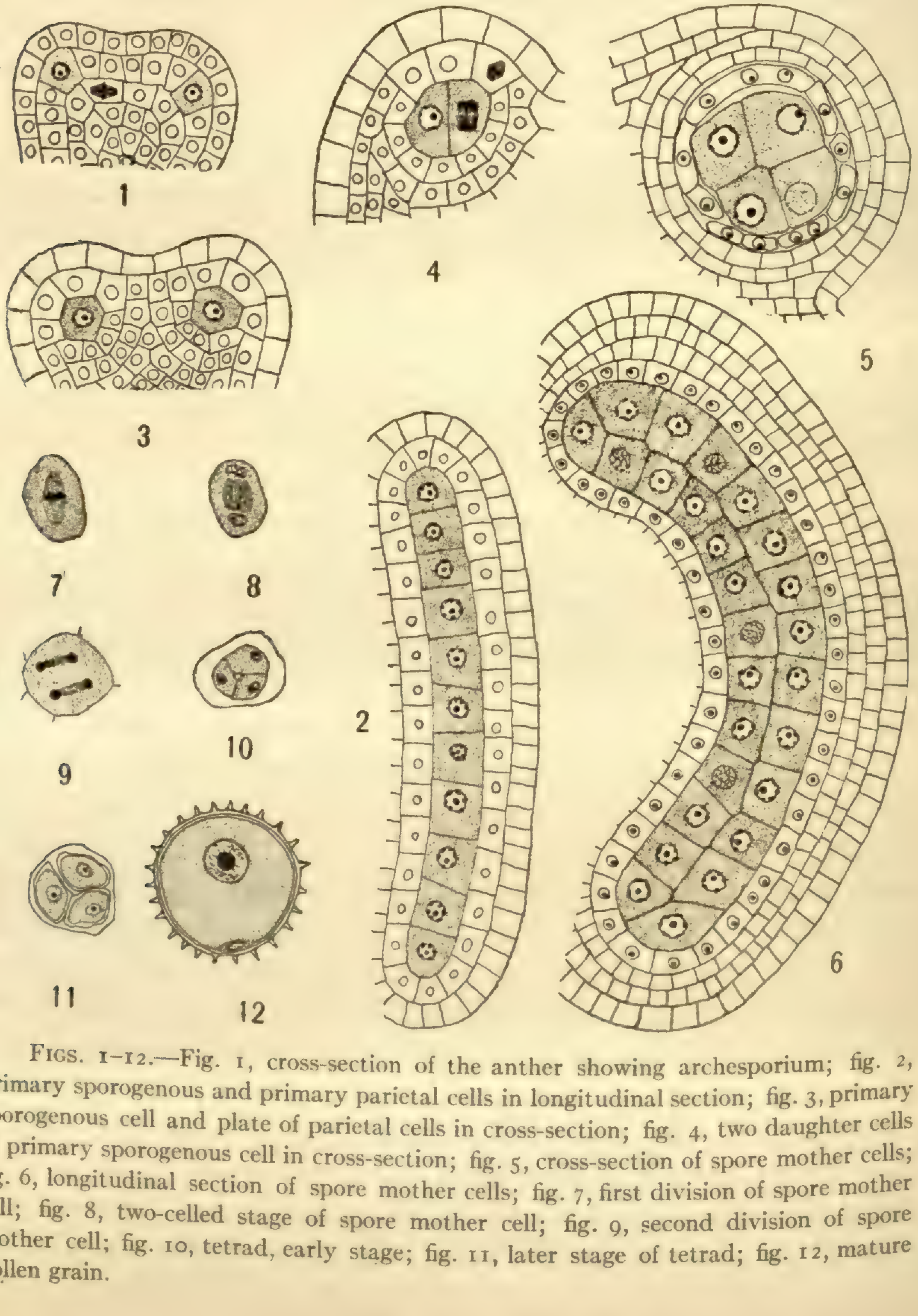
microsporangia in an anther, *Abutilon* resembles *Althaea* (**2, 4**), *Hamamelis* (**13**), *Elodea* (**12**), the Asclepiadaceae, etc.

In cross-section the archesporium is a single hypodermal cell (fig. 1). An apparent exception to this was observed in a few cases where two or three hypodermal cells, because of their size and reaction to stains, might be considered archesporial in their possibilities. The subsequent history of the anther, however, shows that there is only one true archesporial cell as seen in cross-section. While a longitudinal section of the archesporium was not observed, it is very evident that it consists of a single row of several cells, since such a section shows the primary parietal and primary sporogenous cells lying in single rows the full length of the anther (fig. 2). This condition in *Abutilon* agrees with that reported for the Malvaceae and most Compositae, and also for *Gaura* (**14**). The archesporial cells divide, as usual, by periclinal walls to form the primary parietal and primary sporogenous cells (fig. 3).

The primary sporogenous cells initiate two successive divisions, one radial and the other periclinal (figs. 4 and 5). Each primary sporogenous cell, therefore, as a rule produces only four mother cells, these four cells being almost regularly shown in a cross-section of the microsporangium (fig. 5). Thus there is quite a contrast between *Abutilon* and *Althaea rosea* (**2**), since in the latter only a single mother cell is usually to be found in a cross-section of the microsporangium, and in *Malva* also the mother cell is reported to develop directly from the primary sporogenous cell.

As may be seen from fig. 4, there are usually two parietal layers in the stage immediately preceding the formation of the mother cells. Fig. 5 shows the spore mother cell just previous to the tetrad formation. At this stage there are three parietal layers including the tapetum, which is well developed. In its origin the tapetum is like that of *Asclepias Cornuti* (**10**), *Silphium* (**9**), and other forms; and the same account is evidently true for *Althaea*, as may be judged from SACHS's figure (**2**, fig. 377). The tapetum reaches its highest development about the time of the tetrad formation, as is true in most angiosperms. Its development is much later than that of the tapetum of *Euphorbia* (**8**).

At about the time the mother cells are dividing or a little earlier, the nuclei of some of the tapetal cells divide without the formation of cell walls, and tapetal cells with one, two, or three nuclei are found, being much like those described for *Hamamelis* (13), *Ipomoea purpurea* (19), and *Ulmus* (15) in this respect.



FIGS. 1–12.—Fig. 1, cross-section of the anther showing archesporium; fig. 2, primary sporogenous and primary parietal cells in longitudinal section; fig. 3, primary sporogenous cell and plate of parietal cells in cross-section; fig. 4, two daughter cells of primary sporogenous cell in cross-section; fig. 5, cross-section of spore mother cells; fig. 6, longitudinal section of spore mother cells; fig. 7, first division of spore mother cell; fig. 8, two-celled stage of spore mother cell; fig. 9, second division of spore mother cell; fig. 10, tetrad, early stage; fig. 11, later stage of tetrad; fig. 12, mature pollen grain.

The tapetal cells having two or three nuclei are generally more or less elongated (fig. 5).

The spore mother cell is a much prolonged stage, and the second reduction division follows very closely after the first, no walls being formed until after the four nuclei have appeared (figs. 8 and 9), a condition characteristic of the dicotyledons. The tetrad is tetrahedral in arrangement (figs. 10 and 11), no exceptions being observed.

Special study was not made of the composition of the wall of the developing microspores, but evidently it is similar to the microspore walls of *Althaea* (**6**), *Malva* (**5**), and *Ipomoea* (**19**). Since the tapetum reached its highest development during the formation of the tetrad, the mother cells do not become isolated early, but remain intact as in *Althaea* (**1, 2**). While the spore walls are being formed, the tapetum begins to disorganize, but does not entirely disappear until the pollen grains are practically mature. In this respect *Abutilon* resembles *Oenothera* (**17**), *Gaura Lindheimeri* (**14**), etc.

The mature pollen grain is spherical, has both intine and exine well developed, and is covered with spines (fig. 12). Only two nuclei, the tube nucleus and the generative nucleus, were found in the mature pollen grain.

Summary

Abutilon Theophrasti shows the single row of archesporial cells that has been reported for the other two investigated species of Malvaceae, and in the formation of primary parietal and primary sporogenous layers there is also great similarity.

In *Abutilon*, however, each primary sporogenous cell produces four mother cells, while in the other Malvaceae studied only one is formed.

The mother cell stage in *Abutilon* persists until three parietal layers, the inner being a well developed tapetum, are fully formed, after which the characteristic heterotypic and homotypic divisions take place rapidly.

This period of tetrad formation is marked by a multiplication of nuclei in the tapetal cells.

The arrangement of the microspores in the tetrad is tetrahedral and very regular. The tapetum continues to inclose the microspores until they develop their own cell walls and the wall of the mother cell disorganizes, when the tapetal cells gradually disappear. This long persistence of the tapetum is also true of *Althaea rosea*.

The spherical pollen grain of *Abutilon* agrees with that of other described Malvaceae in the number of nuclei and the structure and composition of the walls.

This work has been done in the Botanical Laboratory of the University of Cincinnati, under the direction of Professor H. M. BENEDICT, whom the writer wishes to thank for suggestions and criticisms. Much of the literature was reviewed at the Lloyd Library of Cincinnati, and the writer desires to acknowledge favors received from Mr. WM. HOLDEN, the librarian.

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BRIEFER ARTICLES

ARTIFICIAL PRODUCTION OF ALEURONE GRAINS

(WITH ONE FIGURE)

As is well known, aleurone grains consist mainly of protein material which may be wholly amorphous or partly amorphous and partly crystalline. In the latter case each grain consists typically of a crystal of protein (crystalloid), and an envelope of amorphous protein material whose outer layer may be differentiated from the rest. There is usually included in the envelope a globule of mineral matter or organic material combined with mineral matter (globoid). The variations occurring in different plants have been fully described by PFEFFER.[1]

Each grain is laid down in a vacuole in the protoplasm through the activity of the protoplasm itself. Its manufacture is therefore a distinctly vital process. It is the object of this paper to show that bodies of the same structure may be produced artificially. The resemblance is so striking as to leave little doubt that the essential features of the natural process have been successfully imitated.

The first step in the procedure is the preparation of protein according to the following method of OSBORNE.[2] Half a pound of *Bertholletia* nuts, after the shells have been removed, are ground into a pulp. The fatty material is then removed by repeated thorough treatments with ether, the small portion of the solvent which remains in the solid after the final decantation being allowed to evaporate completely. To the dry residue is added four or five times its volume of 10 per cent NaCl solution in which it stands some hours. Frequent shaking accelerates the dissolving of the protein. The solution of protein is then decanted and thoroughly filtered. At first the finer particles come through, but on repeated filtering through the same paper there results an absolutely clear liquid which microscopic examination shows to be without particles of any kind. This clear filtrate is placed in a dialyzer, and after some hours the sodium chloride is sufficiently removed to cause the precipitation of the protein.

Most of the protein is precipitated as clear, well formed crystals of the hexagonal system. Their thickness is usually about one-sixth

[1] PFEFFER, W., Jahrb. Wiss. Bot. **8**: 429. 1872.

[2] OSBORNE, T. B., Amer. Chem. Jour. **14**: 622. 1892.

of their width. Truncated crystals are common, especially those in which one side is about half as long as the opposite side.

Among the naked crystals are others which are furnished with an envelope (fig. 1, *a*, *b*, *g*); the whole then resembles an aleurone grain. The inclosed crystals may resemble any of the free forms, but are usually complete hexagonal crystals. They may also be of various sizes, but are usually about the size of the natural aleurone grain. Rarely more than one enters into the composition of a single grain (fig. 1, *h*), as happens also in some kinds of natural grains.

The envelope varies in thickness independently of the size of the crystal. It is usually arranged symmetrically about the latter, but the truncated crystals have a tendency to occur at one side. The outline of the grain is then globular or slightly elliptical, but not angular. Occasionally the outermost layer of the envelope differs from the rest in being more opaque and slightly granular (fig. 1, *g*), when it takes the form of a narrow but distinct membrane. This resembles the similar structure sometimes found in natural aleurone grains.

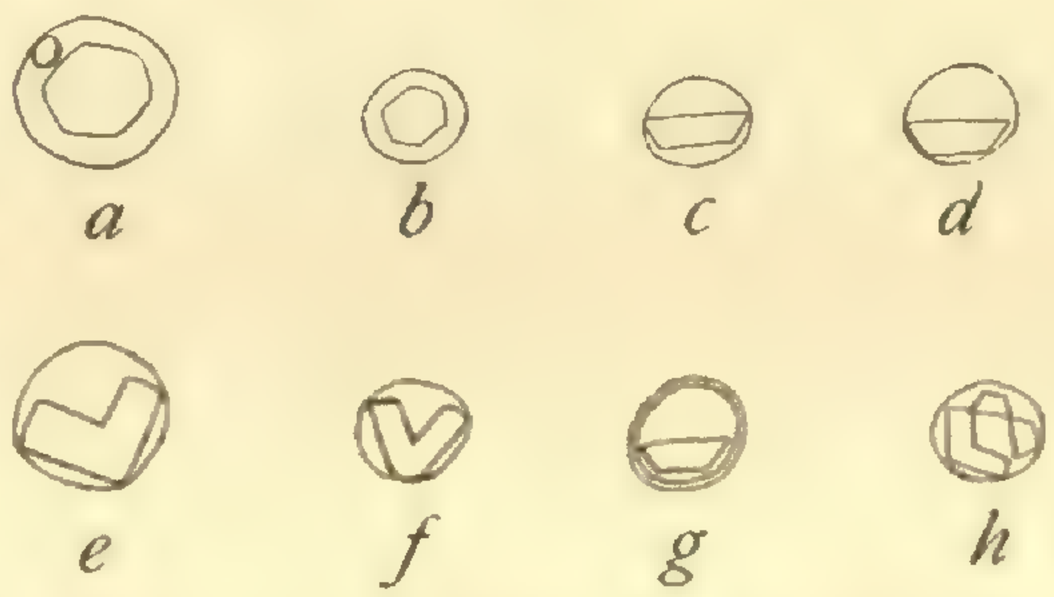

FIG. 1.—Artificial aleurone grains: *a*, protein crystal surrounded by an amorphous protein envelope in which is included a drop of oil which in size and position resembles a globoid; *b*, similar body without an oil drop; *c*–*h*, various forms of crystals resembling those which occur in natural aleurone grains; *g*, the amorphous envelope with a differentiated outer layer such as occurs in some natural grains; *h*, grain containing three crystals, a condition sometimes found in natural grains.

In an experiment in which some fatty matter had not been removed by the ether, many extremely small oil droplets came through the filter and were deposited with the artificial grains. A small number of these had been incorporated into the grains, each of which then consisted of a crystal, an oil droplet, and an envelope. The oil droplet thus resembled the globoid of the natural aleurone grain and the whole artificial grain was extremely similar in appearance to the natural one. In view of this it seems very probable that artificial globoids could easily be produced as inclusions in the artificial aleurone grains by causing dissolved globoid material to precipitate during the formation of the protein crystals. But this did not seem to be sufficiently important to warrant any special effort directed to this end, particularly as globoids do not always accompany the crystals in natural aleurone grains.

The yield of artificial grains varies exceedingly in different experiments. Though two experiments may be performed apparently in exactly the same manner, the number of grains obtained may be vastly different; indeed in some experiments scarcely any are produced. As a rule the first solution extracted from any given preparation gives the best results.

Chemical tests show that the grains are composed of protein, for they respond strongly to all the protein tests such as the xanthoproteic, Millon's, etc. In each test the envelope responded just as strongly as the crystal; it consists, therefore, of uncrystallized protein. With other chemical reagents their behavior is that which is to be expected; they are insoluble in water, alcohol, and sodium carbonate, soluble in weak acids and alkalies and in salt solutions. No marked difference could be observed between the solubility of the envelope and that of the crystal.

Under the action of putrefying bacteria, however, the behavior of the envelope and crystal is occasionally different. In some cases the crystal was dissolved out, leaving the ruptured envelope free; the latter then became flattened out or turned back at the edges.

In the presence of a disinfectant to prevent putrefaction, the grains usually remain unchanged indefinitely. Sometimes, however, the envelope becomes more or less angular, the angles corresponding to those of the crystal.

The proteids of other seeds were used in these experiments, but in no case could artificial grains be obtained. Castor bean, hemp, and lupine gave only crystals without envelopes.

In the case of *Bertholletia*, however, it seems evident that structures resembling the aleurone grains formed through the activity of the protoplasm have been produced in the laboratory. This imitation consists not only in reproducing what is probably the same chemical compound, but also in reproducing the same morphological structure.

In conclusion I wish to acknowledge my indebtedness to Professor W. J. V. OSTERHOUT, in whose course in plant physiology the original observation was made, and with whose advice the subsequent work was done.—W. P. THOMPSON, *Harvard University*.

CURRENT LITERATURE

NOTES FOR STUDENTS

Metabolism of fungi.—Recently a number of papers on the metabolism of fungi have appeared, which, although they represent various phases of the subject, may be noted here in a collective review. Since PASTEUR's discovery of the biological method for separating stereoisomeric components from their racemic compounds, the study of the action of fungi on compounds having asymetric carbon atoms has been of great interest. The work of the earlier investigators, like that of LE BELL, LEUKOWITSCH, SCHULZE and BOSSHARD, and others, was concerned chiefly with the chemical aspects of the subject, with the purpose of resolving racemic compounds into their optically active components.

Taking up the subject more in its biological aspect, for the purpose of determining whether any fungi are able to utilize both components of racemic compounds to an equal extent, PRINGSHEIM[1] has investigated the action of 16 fungi and 2 bacteria on leucine and glutaminic acid, from which SCHULZE and BOSSHARD[2] had obtained *d*-leucine and *l*-glutaminic acid by the action of *Penicillium*. PRINGSHEIM found that in all cases both of the components of the amino-acids used were partly consumed by the organisms. In about one-half of the experiments both components were consumed to an equal degree, so that the recovered portions of the acids were optically inactive. In the remaining instances one isomer was consumed to a greater extent than the other, the naturally occurring component being the one consumed most readily in all such cases.

HERZOG and his students have taken up the study of the action of fungi on *d*-*l*-oxyacids and *d*-*l*-amino-acids in order to gain a knowledge of the process involved in the utilization of one of the isomers of the inactive forms of these acids. The experimentation was carried out both with living fungi and with mycelia killed by various means. In the experiments with living material the fungi were grown in flasks of suitable culture media until the carbon dioxide production became constant. A definite quantity of the acid to be tested was then introduced into the flasks and the subsequent carbon dioxide output determined. At the end of the experiment the residual acid was

[1] PRINGSHEIM, HANS, Studien über Spaltung racemischer Aminosäuren durch Pilze. Zeitschr. Physiol. Chem. **65**:96–109. 1910.

[2] SCHULZE, E., und BOSSHARD, E., Untersuchungen über die Aminosäuren welche bei der Zersetzung der Eiweissstoffe durch Salzsäure und durch Barytwasser entstehen. II. Zeitschr. Physiol. Chem. **10**:134–145. 1886.

determined and its rotation measured. In the experiments with fungi killed by acetone, methyl alcohol, or other means, the powdered fungus material was added to flasks containing solutions of the acids. The carbon dioxide products and residual acid were determined as before.

In the first experiments reported by HERZOG and MEIER[3] it was found that the addition of lactic, tartaric, malic, mandelic, and β-oxybutyric acids to cultures of *Penicillium glaucum*, in which the carbon dioxide production had become fairly constant, resulted in a great increase of the carbon dioxide output. In every case the excess of carbon dioxide over the normal was much greater than that calculated on the assumption that all of the acid used up had been completely oxidized to carbon dioxide and water. Under the same conditions glycollic, citric, pyrotartaric, and oxybutyric acids gave no increase in the carbon dioxide production. The authors suggest that these experiments indicate that the biological splitting of substances containing an asymmetric carbon atom depends on a process of oxidation. Only the acids having an asymmetric carbon atom were oxidized.

To test this hypothesis further, experiments were carried out with fungous material killed with acetone and methyl alcohol and finely pulverized. Definite quantities of the material were added to flasks containing solutions of lactic acid or sodium lactate, and also to control flasks containing distilled water. It was found that the carbon dioxide production in the flasks containing the acid or its salt was slightly greater than in the controls.

In a second paper[4] the method of experimentation with killed mycelia is applied to the study of a number of other acids. The mycelia in these experiments were immersed in liquid air, by which, it was assumed, the cells were killed, although the spores were subsequently found to be alive. In these experiments it was found that *d*-tartaric acid, *l*-tartaric acid, and *d-l*-tartaric acid were oxidized, while mesotartaric acid, which is not separable into optically active components, was left intact. The dextro-rotatory form was oxidized most rapidly. The optically active isomers of lactic acid showed scarcely any difference in the rate of oxidation, while *l*-mandelic acid was oxidized more rapidly than its antipode. Glycollic acid, having no asymmetric carbon atom, was not attacked. The authors conclude that the preferential oxidation of one component of a racemic mixture, which has heretofore been regarded as biological selections of food substances, is merely the result of differences in the reaction velocities of the antipodes with the substances of the organisms.

In continuation of the foregoing work, HERZOG and RIPKE[5] have studied

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[3] HERZOG, R. O., und MEIER, A., Ueber Oxydation durch Schimmelpilze. Zeitschr. Physiol. Chem. **57**: 35–42. 1908; also MEIER, A., Dissertation under the same title. Karlsruhe. 1909.

[4] ———. *Ibid.* **59**: 57–62. 1909.

[5] HERZOG, R. O., und RIPKE, O., Ueber das Verhalten einger Pilze zu organischen Säuren. *Ibid.* **73**: 284–289. 1911.

the effects of *Oidium lactis* killed with acetone and ether on the lactic, succinic, and mandelic acids. The results obtained do not conform with those obtained in the foregoing experiments with *Penicillium*. Only lactic acid gave a greater carbon dioxide production than the control with distilled water. With mandelic and succinic acids the control flasks yielded greater amounts of carbon dioxide. In an experiment in which the fungus was left in liquid air for several hours, subsequent cultures showed that the cells had not all been killed.

A similar set of experiments carried out by HERZOG, RIPKE, and SALADIN[6] with acetone preparations of *Mycoderma cerevisiae* showed that with acetic acid and lactic acid the carbon dioxide production was less in the acid medium than in distilled water, although a part of the acid in each case had disappeared. The carbon dioxide output in experiments with the different isomeric modifications of mandelic and tartaric acids was not determined, but the whole added quantity of these acids could not be recovered. In some cases with mandelic acid the total acid content of the controls at the end of the experiment was as great as that in flasks to which acid had been added. The authors assume that the autolytic production of acid by the killed fungus cells reaches a certain maximum. If that maximum has been attained by the addition of a foreign acid, no further spontaneous acid formation occurs. Succinic acid depressed the production of carbon dioxide, but there was no evidence that any of the acid had disappeared. The general conclusion from this last set of experiments is that the production of carbon dioxide by killed cells of *Mycoderma* is depressed in acid media, although the quantity of acid is diminished. The disappearance of the acid, therefore, cannot be explained as a process of oxidation, nor is the process one of metabolism, since the cells were dead. In view of the comparatively small quantities of acids which disappeared apparently through the action of the killed fungus cells, the experiments would have been more convincing if the authors had reported control experiments showing how much of the acids could be immediately recovered from the mixtures.

In another paper by HERZOG and SALADIN[7] the effect of leucine on the carbon dioxide production of *Penicillium* is reported. The method of experimentation was similar to that described above in the experiments of HERZOG and MEIER, and the results were comparable to those obtained with oxyacids. The addition of leucine was followed by an increased production of carbon dioxide, which was greater than that calculated on the assumption that all the available leucine had been oxidized to carbon dioxide and water.

The important series of researches of EHRLICH[8] on the behavior of amino-

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[6] HERZOG, R. O., RIPKE, O., und SALADIN, O. *Ibid.* **73:** 290–301. 1911.

[7] HERZOG, R. O., und SALADIN, O., Ueber das Verhalten einiger Pilze gegen Aminosäuren. *Ibid.* **73:** 302–307. 1911.

[8] For a general account of this work see EHRLICH, F., Ueber die chemischen Vorgänge pflanzlichen Erweissstoffwechsels und ihre Bedeutung für die Alkoholische Gärung und andere pflanzenphysiologische Processe. Landwirth. Jahrb. **38:** 289–327. 1909.

acids in alcoholic fermentation has greatly advanced our knowledge of the origin of fusel-oils, which have usually been regarded as side-products of sugar fermentation. These investigations have been extended by EHRLICH and JACOBSON[9] to other fungi, to determine whether the decomposition of amino-acids induced by them is similar to that brought about by the yeast cell. The authors have studied the action, on amino-acids, of some 50 fungi, upon which a complete report is promised. The behavior of the filamentous fungi toward amino-acids differs greatly according to whether carbohydrates are present or not. In the absence of carbohydrates the decomposition of amino-acids is more extensive than that produced by yeasts, but in the presence of carbohydrates the degree of decomposition differs with different fungi. In the present paper the peculiar behavior of *Oidium lactis* on amino-acids in the presence of sugar is reported. The action of this fungus results in the replacement of the amino-groups by hydroxyl, thereby yielding oxyacids corresponding to the amino-acids according to the following general reaction:

$$R \cdot CH(NH_2)CO_2H + H_2O = R \cdot CH(OH)CO_2H + NH_3$$

The ammonia which is formed is used in protein synthesis by the fungus. Here as with the yeast cell the amino-nitrogen (in the form of ammonia) enters into the metabolism of the cell, while the rest of the molecule is excreted as a product not capable of being further utilized. The end products in the two cases are different, being in the case of the yeast cell an alcohol with one carbon less than the amino-acid from which it was derived, while with *Oidium lactis* an oxyacid corresponding to the amino-acid results. By the action of *Oidium lactis*, *l*-tyrosin yielded *d*-paraoxyphenyl-lactic acid, *d-l*-phenylalanin yielded *d*-phenyl-lactic acid, and *l*-tryptophan gave *l*-indol-lactic acid, all acids which were heretofore not known in those modifications.

In this connection the authors point out that KOTAKE[10] obtained from dogs suffering from phosphorus poisoning the levorotatory form of oxyphenyl-lactic acid, thus affording an example of the production by the plant and by the animal cell, not of the same but of opposite stereoisomers from one and the same substance. It should be stated, however, that KOTAKE himself regards it as extremely improbable that his acid was produced from tyrosin, as he was unable to isolate oxyphenyl-lactic acid as a result of feeding tyrosin itself.

A better example of the production of isomeric antipodes from the same racemic substance is afforded by the action of plant cells and of animal cells on racemic phenylamino-acetic acid. NEUBAUER and WARBURG[11] obtained the

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[9] EHRLICH, FELIX, und JACOBSON, K. A., Ueber die Umwandlung von Aminosäuren in Oxysäuren durch Schimmelpilze. Ber. Deutsch. Chem. Gesells. **44**: 888–897. 1911.

[10] KOTAKE, Y., Ueber *l*-Oxyphenylmilchsäure und ihr Vorkommen im Harn bei Phosphorvergiftung. Zeitschr. Physiol. Chem. **65**: 397–401. 1910.

[11] NEUBAUER, O., und WARBURG, O., Ueber eine Synthese mit Essigsäure in der künstlich durch bluteten Leber. *Ibid.* **70**: 1–9. 1910.

d-acetylphenylamino-acetic acid from this substance injected into the liver of dogs, while NEUBAUER and FROMHERZ[12] obtained the *l*-acetylphenylamino-acetic acid as a result of yeast fermentation of the same racemic compound.

The intermediate chemical transformations by which *d*-amino-acids are changed into alcohols with one carbon atom less in fermentation have been investigated by NEUBAUER and FROMHERZ and described in the paper cited above. The content of the paper is largely chemical. The conclusion is reached that the amino-acids are not directly transformed into alcohols by hydrolysis and subsequent splitting off of ammonia and carbon dioxide, as represented by the general formula

$$R \cdot CH \cdot NH_2 - COOH + H_2O = R \cdot CH_2OH + CO_2 + NH_3$$

but that keto-acids are first formed, and these, by loss of carbon dioxide and reduction, are changed into alcohols, the main steps of the process being represented as follows:

$$R - CHNH_2 - COOH + O = R - CO - COOH + NH_3$$
$$R - CO - COOH \rightarrow R \cdot CHO + CO_2$$
$$R - CHO + {}_2H = R - CH_2OH$$

This interpretation is the result of experiments in which it was shown (1) that a keto-acid (phenylglyoxylic acid) was formed by the fermentation of phenyl-amino-acetic acid, and (2) that a keto-acid (*p*-oxyphenylpyrotartaric acid) yielded the same alcohol by fermentation as the corresponding amino-acid (tyrosin).[13] A number of side reactions and secondary products occur in this process. The occurrence of the aldehyde is postulated. According to the authors the decomposition of amino-acids by yeasts is hereby shown to follow the same course as the decomposition of these acids in the animal body, except that the postulated aldehyde which is reduced to alcohol by the yeast cell is oxidized to the corresponding fatty acid which is further utilized in metabolism by the animal cell.

The discovery by EHRLICH[14] of the production of fumaric acid from sugar through the agency of *Rhizopus nigricans* is of great biological interest, not only because it is the first instance of the occurrence of fumaric acid as a product of metabolism of micro-organisms, but also because of its possible bearing on the origin of unsaturated acids in higher plants. The acid was isolated by EHRLICH from culture solutions, containing much sugar, upon which *Rhizopus nigricans* was grown. The quantity of acid varies with the sugar content, but in old cultures from which the sugar has disappeared the acid is again consumed.

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[12] NEUBAUER, O., und FROMHERZ, K., Ueber den Abbau der Aminosäuren bei der Hefegärung. Zeitschr. Physiol. Chem. **70:** 326-350. 1911.

[13] EHRLICH, FELIX, Ueber die Vergärung des Tyrosins zu *p*-Oxyphenyl-äthyl-alkohol (Tyrosol). Ber. Deutsch. Chem. Gesells. **44:** 139–146. 1911.

[14] ———, Ueber die Bildung von Fumarsäure durch Schimmelpilze. Ber. Deutsch. Chem. Gesells. **44:** 3737–3742. 1911.

With glycerin, alcohol, or peptone as sources of carbon, no fumaric acid is produced. The fact that fumaric acid here occurs as an intermediate product in the metabolism of sugar suggests that unsaturated acids in higher plants may result from carbohydrate metabolism. That a close relation exists between the higher unsaturated acids and carbohydrates in plant metabolism has been generally conceded by plant physiologists since the work of MAQUENNE.

That many fungi and bacteria are able to utilize fats has been shown by several investigators. A further contribution to the subject has been made by OHTA,[15] who studied the decomposition of the fat of horse liver caused by five forms of fungi obtained by exposing culture plates in the laboratory. The forms were *Cladosporium herbarum*, *Penicillium glaucum*, *Aspergillus glaucus*, *A. nidulans*, and *Actinomucor repens*. All of these caused the disappearance of fat from the ground sterilized liver tissue. *Actinomucor* was the most active, causing the disappearance of over 60 per cent of the fat in three weeks. Of the others, *Aspergillus* used 17–20 per cent, *Cladosporium* 14 per cent, and *Penicillium* 6–8 per cent. Attempts to grow *Actinomucor* on culture solutions containing fat as the only source of carbon, in order to study the mode of decomposition of the fat, were unsuccessful. The paper contains detailed notes on the methods and precautions to be observed in making fat determinations in work of this kind.

Another contribution to the subject of the utilization of fat by fungi has been made by ROUSSY,[16] who experimented with the following forms: *Absidia glauca*, *Circinella umbellata*, *Mucor mucedo*, *Phycomyces nitens*, *Rhizopus nigricans*, *Sporodinia grandis*, *Morteirella candelabrum*, *Aspergillus flavus*, *Citromyces glaber*, *Penicillium luteum*, *Sterigmatocystis nigra*, and *Sporotrichum bombyceum*. All of these grew well on fats and oils of various kinds. To determine if it was the fatty acid or the glycerine which was utilized, cultures were made in Raulins solution in combination with oleic, palmitic, or stearic acid or glycerine. It was found that the fungi thrived well on the fatty acids, but only *Aspergillus* and *Penicillium* grew on glycerin solutions.

REICHEL, studying the effects of acetic acid and its salts on a form of *Penicillium*, has rediscovered the fact that the toxicity of that acid is mainly due to the action of the undissociated molecule. He finds that acetic acid is poisonous in much lower concentrations than those at which the strong mineral acids are toxic, but, owing to its slight dissociation, its toxicity cannot be attributed to the hydrogen ion. At the same time, the salts of acetic acid, which are highly dissociated, are not poisonous, hence the acetate ion is not poisonous. The toxicity of acetic acid, therefore, must be attributed to the molecule as a whole.

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[15] OHTA, KOHSHI, Ueber die fettzehrenden Wirkungen der Schimmelpilze nebst dem Verhalten des Organfettes gegen Fäulniss. Biochem. Zeitschr. **31**: 177–194. 1911.

[16] ROUSSY, A., Sur la vie des Champignons dans les acides gras. Compt. Rend. **153**: 884–886. 1911.

The same conclusion reached by CLARK[17] by similar experimentation and reasoning many years ago seems to have escaped his notice.

REICHEL[18] further points out that the addition of mineral acids to solutions containing acetates produces the same effect as the addition of acetic acid, since the acetic acid is replaced in its salts by the stronger acids and undissociated acid is formed in the solution as a result of the establishment of a new equilibrium. In solutions whose acidity is not great enough to inhibit growth entirely, the author finds a certain regulatory depression of the acidity by the fungus until more favorable concentrations are attained. This phase of the subject seems to demand further investigation to determine whether such purposeful regulation really exists. Under certain conditions, at any rate, depending upon the substances available in the medium, either acid or alkali will accumulate in culture solutions through the action of fungi to such a degree as to inhibit growth entirely.[19]

BORKORNY[20] reports a number of miscellaneous experiments and observations indicating that methyl alcohol can be used as a source of carbon by some fungi and bacteria. A yeast not capable of fermenting cane sugar or glucose grew spontaneously on a solution of mineral nutrients to which 0.1 per cent of methyl alcohol had been added. Inoculations from this culture were made in solutions containing 0.0025 per cent to 5 per cent methyl alcohol. After a time the flasks contained vegetations of yeast and bacteria and in some cases infusoria were present. Apparently no precautions were taken to avoid contamination, so that it is possible that carbon compounds were introduced in the form of dust particles.

SAITO[21] reports the formation of lactic acid by *Rhizopus chinensis*, thus confirming the observations of EIJKMAN and of CHRZASZCZ, who reported the production of lactic acid by *Rhizopus Rouxii*. These observations had been doubted because other instances of the production of lactic acid by filamentous fungi are not known. SAITO identified his acid by means of the zinc and the calcium salts and by the reaction of UFFELMAN.

GOUPIL[22] finds that *Rhizopus Rouxii* produces in cultures up to 4 grams

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[17] CLARK, J. F., On the toxic effect of deleterious agents on the germination and development of certain filamentous fungi. BOT. GAZ. **28:** 289–327; 378–404. 1899.

[18] REICHEL, J., Ueber das Verhalten von *Penicillium* gegenüber der Essigsäure und ihren Salzen. Biochem. Zeitschr. **30:** 152–159. 1910.

[19] HASSELBRING, H., The carbon assimilation of *Penicillium*. BOT. GAZ. **45:** 176–193. 1908.

[20] BORKORNY, TH., Beobachtungen über Pilze, welche Methylalkohol als C-Quelle verwenden können. Centralbl. Bkt. II. **29:** 176–188. 1911.

[21] SAITO, K., Ein Beispiel von Milchsäurebildung durch Schimmelpilze. Centralbl. Bakt. II. **29:** 289–290. 1911.

[22] GOUPIL, R., Recherches sur *l'Amylomyces Rouxii*. Compt. Rend. **153:** 1172–1174. 1911.

per liter of succinic acid mixed with some acetic and some butyric acid. Contrary to the statements of some workers, oxalic and lactic acids are not produced. He believes that the succinic acid is formed from sugar and not from any amino-acid.—H. HASSELBRING.

Current taxonomic literature.—G. E. OSTERHOUT (Muhlenbergia **8**:44, 45. 1912) characterizes a new *Cogswellia* (*C. concinna*) and a new variety of *Gnaphalium* (*G. decurrens* var. *glandulosum*) from Colorado.—O. PAULSEN (Arb. Bot. Have Kb. no. 65. 303–318. 1911) under the title "Marine plankton from the East-Greenland Sea" records the Peridiniales found on the Danish Expedition to Greenland in 1906–1908 and describes a new species of *Peridinium* (*P. varicans*), also a new species doubtfully referred to *Apodinium*.—W. H. RANKIN (Phytopathology **2**:28–31. *pl. 3.* 1912) describes and illustrates a new fungus (*Sclerotinia Panacis*) which is said to be the cause of a root-rot of ginseng; it was found near Apulia, N.Y.—A. B. RENDLE, E. G. BAKER, S. MOORE, and A. GEPP (Journ. Linn. Soc. Bot. **40**:1–245. *pls. 1–7.* 1911) have published an important paper entitled "A contribution to our knowledge of the Flora of Gazaland." The paper includes a general descriptive account of the country concerned, records about 1000 species of which approximately 180 are new to science. The plants were collected by Mr. C. F. M. SWYNNERTON and the types are deposited in the herbarium of the British Museum.—R. A. ROLFE (Bot. Mag. *t. 8417.* 1912) describes and illustrates a new species of *Stanhopea* (*S. peruviana*) from Peru, and (Kew Bull. 131–135. 1912) has published several new species of orchids including 4 from Panama and South America.—E. ROSENSTOCK (Rep. Sp. Nov. **10**:274–280. 1912) under the title "Filices costaricenses" has published 11 new species of ferns.—P. A. RYDBERG (Torreya **12**:1–11. 1912) in continuation of studies of the plants collected on the Peary arctic expeditions gives a list of the plants secured by Drs. WOLF and GOODSELL; the article includes a new species of *Conioselinum* (*C. pumilum* Rose) from Labrador. The same author (Bull. Torr. Bot. Club **39**:99–111. 1912) under "Studies on the Rocky Mountain flora XXVI" describes a new species in *Deschampsia* and one in *Anticlea*. Two new generic names are proposed, namely *Hesperochloa*, based on *Poa* (?) *Kingii* Wats., and *Dipterostemon*, based on *Brodiaea capitata* Benth.—C. S. SARGENT (Rep. Mo. Bot. Gard. **22**:67–83. 1911) under the heading "Crataegus in Missouri II" has described 14 new species.—A. K. SCHINDLER (Rep. Sp. Nov. **10**:403, 404. 1912) has published a new genus (*Kummerowia*) based on *Hedysarum striatum* Thunb. a species common to the New and Old World.—H. SCHINZ (Vierteljahrsschrift Naturf. Gesells. Zürich **56**:229–268. 1911) in an article "Beiträge zur Kenntnis der afrikanischen Flora" has proposed the following new genera belonging to the Amarantaceae: *Centemopsis*, *Nelsia*, *Neocentema*, and *Lopriorea*.—R. SCHLECTER (Rep. Sp. Nov. **10**:248–254, 291–296, 352–363, 385–397, 445–461. 1911–1912) under the title "Orchidaceae novae et criticae" has published about 70 new species of orchids from Central and

South America. One new genus (*Neokoehleria*) is included from Peru.—The same author (Orchis **6**:6–10. *pl. 1.* 1912) has published new species of orchids, 2 of which are from Colombia.—F. J. Seaver (Mycologia **4**:45–48. *pl. 57.* 1912) gives an account of the genus *Lamprospora* and adds 2 new species.—C. P. Smith (Muhlenbergia **7**:136–138. 1912) records a new variety of violet (*Viola Beckwithii* var. *cachensis*) from northern Utah.—O. Stapf (Hooker's Ic. IV, **10**: *t. 2947.* 1911) describes and illustrates a new genus (*Teonongia*) of the Moraceae from Tonkin; the same author (*ibid. tt. 2949, 2950*) describes and illustrates two new genera (*Lintonia* and *Dignathia*) of the Gramineae from British East Africa.—P. C. Standley (Proc. Biol. Soc. Wash. **24**:243–250. 1911) presents a synopsis of the American species of *Fagonia*, recognizing 12 species, 4 of which are new to science. The same author (Smith. Misc. Coll. **56**: no. 33. 1–3. 1912) has described 3 new species of flowering plants from Alberta, and (*ibid.* no. 34. 1–3. *pl. 1*) describes and illustrates a new species of *Viorna* (*V. Ridgwayi*) from southern Illinois.—F. Stephani (K. Sv. Vet. Akad. Handl. **46**: no. 9. 1–92. 1911) presents the results of an investigation of the Hepaticae collected on the Swedish expedition to Patagonia and Tierra del Fuego in 1907–1909; about 145 species are described as new to science. The types are deposited in the herbarium of the Botanical Museum at Upsala. The same author (Sp. Hep. **4**:641–736. 1911) continues his treatment of the Hepaticae and includes several new species from America belonging mainly to *Frullania* and *Archilejeunea*.—C. Torrend (Broteria Ser. Bot. **10**:29–49. 1912) under the title of "Deuxième contribution pour l'étude des champignons de l'ile de Madère" describes several species new to science and proposes a new genus (*Vermiculariopsis*) of the Sphaeropsidaceae. —W. Trelease (Rep. Mo. Bot. Gard. **22**:37–65. *pls. 18–72.* 1911) presents an illustrated account of the agaves of Lower California with a synopsis of the 25 reorganized species of which 17 are new to science; and (*ibid.* 85–97. *pls. 73–99*) gives a "Revision of the agaves of the group Applanatae," to which group 10 species are referred, 5 being hitherto undescribed; and (*ibid.* 99, 100. *pls. 100–103*) characterizes a new variety of *Agave* (*A. angustifolia* var. *Sargentii*) based on plants in cultivation at the Missouri Botanical Garden; and (*ibid.* 101–103. *pls. 104–108*) records 2 new species of *Yucca* from Texas and adjacent Mexico.—W. Wangerin (Rep. Sp. Nov. **10**:273. 1912) has published a new species of *Mastixia* (*M. philippinensis*) from the island of Luzon, P.I.—E. J. Welsford (Ann. Botany **26**:239–242. 1912) gives an account of an alga found in an aquarium associated with *Azolla caroliniana* which was imported from North Carolina. The author has given the alga the name of *Trichodiscus elegans*.—H. F. Wernham (Journ. Bot. **49**:317, 318. 1911) has published a new genus (*Pteridocalyx*) of the Rubiaceae from Demerara.—Different authors (Kew Bull. 35–44. 1912) have published several new species of flowering plants including 2 new species of *Columnea* from Guatemala and Venezuela, and a new *Zschokkea* from Peru; and (*ibid.* 90–107) under the title "Diagnoses

africanae XLVI" several new species are described, and the following new genera are proposed: *Isoberlinia* and *Paradaniellia* of the Leguminosae, and *Klaineanthus* and *Hamilcoa* of the Euphorbiaceae.—J. M. GREENMAN.

Recent work among Filicales.—DAVIS[23] has investigated the structure of *Peranema* and *Diacalpe*, Asiatic genera of ferns whose relationships have been somewhat doubtful. Both genera are polystelic; and while in *Peranema* the short-stalked sorus is a mixed one, with a receptacle of the Gradatae type and traces of a basipetal succession of sporangia, in *Diacalpe* the mixed sorus shows no traces of basipetal succession. Moreover, in *Peranema* the annulus is slightly oblique, while in *Diacalpe* it "is vertical in insertion, but slightly twisted in its course across the sporangial head." Both show relationships to species of *Nephrodium*, but are most nearly related to *Woodsia* and *Hypoderris*," and fall naturally into the Woodsieae-Woodsiinae group of Polypodiaceae," a group that is regarded as intermediate between Cyatheaceae and the Aspidieae. The conclusion is suggested that the *Aspidium* forms have come from a Gradatae ancestry, and "that *Peranema* and *Diacalpe* are relatively early members of a phyletic drift to the Polypodiaceae."

BOWER[24] has used a study of *Alsophila* (*Lophosoria*) *pruinata* as the basis for a discussion of an important phyletic sequence. *Lophosoria* is shown to be a more primitive type than the true species of *Alsophila* and worthy of generic separation from that genus. The phyletic relations with *Struthiopteris*, *Onoclea*, *Cystopteris*, *Acrophorus*, *Peranema*, *Diacalpe*, *Woodsia*, and *Hypoderris* are discussed and the following "progressions" announced: (1) the frequent dichotomous branching in Gleicheniaceae becomes rarer in the higher types, and the creeping axis of the earlier forms becomes ascending or erect in some of the later ones"; (2) "the peculiarities of the original gleicheniaceous type of leaf are shown in reminiscent details in the Cyatheaceae, but lost elsewhere"; (3) progression from primitive hairs to scales; (4) progression from the protostele of § MARTENSIA of *Gleichenia* to the solenostele of *G. pectinata* and *Lophosoria*, and the polystele of all other members of the series; (5) progression from the Simplices type of sorus (*Gleichenia* and *Lophosoria*) to the Gradatae type in Cyatheaceae, and finally to the Mixtae type in *Hypoderris*, *Peranema*, and *Diacalpe*, "a condition leading probably to that of the Aspidieae"; (6) progression from a larger spore-output and an oblique annulus to a smaller output and a vertical annulus; (7) progression from a larger sperm-output to a smaller one.

This series is believed by BOWER to constitute a true phylum, a phylum quite distinct from that of the ferns with originally marginal sori. The prob-

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[23] DAVIS, R. C., The structure and affinities of *Peranema* and *Diacalpe*. Ann. Botany **26**: 245–268. *pls. 28, 29.* 1912.

[24] BOWER, F. O., Studies in the phylogeny of the Filicales. II. *Lophosoria*, and its relation to the Cyatheoideae and other ferns. Ann. Botany **26**: 269–323. *pls. 30–36.* 1912.

able phyletic sequence of families, therefore is as follows: "Gleicheniaceae, Cyatheaceae (with minor groups, e.g., Woodsieae, etc.), Aspidieae."

Miss HUME[25] has investigated the sieve tubes of *Pteridium aquilinum*, and compared them with those of *Lygodium dichotomum* and *Marsilia quadrifolia*. The xylem has long received intensive study on account of its service in conclusions concerning phylogeny; but there are symptoms that the phloem is now beginning to come into its own. The stock contrasts between the sieve tubes of pteridophytes and spermatophytes are now beginning to break down and Miss HUME has contributed her share to this process. Not only does callus appear, as RUSSOW showed, but the author shows that the pores are not closed. "The outstanding differences are in shape and contents; the sieve tubes of vascular cryptogams are larger and thicker walled and contain refringent granules." The larger size and thicker walls are thought to be associated with the fact that the sieve tubes of pteridophytes (on account of the absence of secondary thickening) have to function for a long time, in some cases for as much as 20 years, while in some dicotyledons and gymnosperms they are renewed each year. The time is at hand when the sieve tubes can be linked up in phyletic sequences as the xylem elements have been.

THOMAS[26] has discovered in the Jurassic of Yorkshire sporangia of *Coniopteris hymenophylloides* Brongn. and *Todites Williamsoni* Brongn., which support the view that the former species is closely related to the modern Cyatheaceae, and which furnish for the latter species additional points of resemblance to the modern *Todea*. Fertile material of *Cladophlebis lobifolia* Phill. was also secured, which justifies its removal from the form-genus and its provisional placing in a new genus *Eboracia*, related in sori and spores to *Coniopteris*, but very distinct in the form of the fertile fronds.—J. M. C.

American cecidology.—All students of the biological sciences will be interested in the increased attention which cecidology is receiving in America, and also in the fact that it is being studied by both entomologists and botanists. FELT presents four papers. In the first[27] he gives a very complete list of plants on which the cecidia of our American gall midges are known to occur and the names of the gall-makers. Our knowledge of this group of gall-makers is very indefinite, and therefore the very brief one-line descriptions may appear unsatisfactory to many who are unfamiliar with the subject. However, the list will prove of very great value to the student of plant pathology and cecidology. In a second paper[28] FELT describes 17 new species of gall midges,

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[25] HUME, E. M. MARGARET, The history of the sieve tubes of *Pteridium aquilinum*, with some notes on *Marsilia quadrifolia* and *Lygodium dichotomum*. Ann. Botany **26**: 573–587. *pls. 54, 55*. 1912.

[26] THOMAS, H. HAMSHAW, On the spores of some Jurassic ferns. Proc. Cambridge Phil. Soc. **16**: 384–388. *pl. 3*. 1911.

[27] FELT, E. P., Hosts and galls of American midges. Jour. Econ. Entomology **4**: 451–475. 1911.

[28] ———, New species of gall midges. *Ibid*. **4**: 476–484. 1911.

but many of them are not true gall-makers while others produce very small and insignificant galls. In a third paper[29] the same author describes three new species of dipterous gall-makers, and in the fourth[30] he describes four new species of gall midges from St. Vincent, West Indies. The development and structural characters of all these galls remains to be worked out by the botanist.

BEUTENMÜLLER[31] has given us another most excellent paper on the North American galls. This last paper is on the genus *Dryophanta*, and contains excellent descriptions of both galls and insects of the 39 known species, with complete synonomy and bibliography. Most of the galls are figured, and all of them occur on oaks, but in a few cases the specific name of the host is not known. The 32 species for which the hosts are given are found on 24 species of oak. *Quercus rubra* leads with 7 species, *Q. alba* has 5, *Q. coccinea* has 4, *Q. undulata*, *Q. velutina*, and *Q. nana* have 3 each, *Q. arizonica*, *Q. marylandica*, *Q. prinoides*, *Q. palustris*, and *Q. laurifolia* have 2 each. *Dryophanta palustris* is found upon 7 different hosts, *D. lanata* on 5, *D. notha* on 3, 5 other species on 2 each, and 24 species on 1 each.

The same author[32] also describes and figures two new species of *Holcaspis* galls from Mexico. These papers will be absolutely necessary for students who wish to make botanical studies of cecidia.

One of the most interesting and important contributions to American cecidology is by ERWIN F. SMITH,[33] who has continued his studies on crown gall of plants, and presents some interesting comparisons with the cancer of human beings. The similarity between plant and animal malformations has attracted the attention of many observers, who have looked upon the study of plant galls as a fruitful field of investigation, but unfortunately very few have gone into it far enough to see the real possibilities. SMITH's confidence in this line of work is expressed as follows: "I believe we have in these particular plant overgrowths a key to unlock the whole cancer situation. In consideration of these discoveries many closed doors in cancer research must now be opened, and studies on the etiology of the disease must be done over with a view to finding a parasite within the cancer cell, and separating it therefrom by an improved technic of isolation." In answer to his critics he claims that the crown gall is not the same as a granulomata of the animal. He also shows that the tendency of the human cancer to form secondary growths by means of strands of tissue is similar to the formation of secondary growth

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[29] FELT, E. P., Three new gall midges. Jour. N.Y. Entom. Soc. **19**:190–193. 1911.

[30] ———, New West Indian gall midges. Entomol. News **23**:173–175. 1912.

[31] BEUTENMÜLLER, WILLIAM, The North American species of *Dryophanta* and their galls. Amer. Mus. Nat. Hist. **30**:343–369. 1911.

[32] ———, Two new species of *Holcaspis* from Mexico. Psyche **18**:86, 87. 1912.

[33] SMITH, ERWIN F., On some resemblances of crown gall to human cancer. Science N.S. **35**:161–172. 1912.

of the crown gall, and believes that "we have in the crown gall a striking analogy to what occurs in malignant animal tumors." He does not claim that the animal cancer and crown gall are due to the same organism. The latter part of the paper is devoted to physiological characters of the organisms and presents some suggestions which will be of importance to the plant physiologist who has the courage to attempt to explain the formation of plant cecidia as a result of irritation by parasitic fungi and insects.—MEL T. COOK.

Inheritance in flax.—TAMMES[34] has studied a number of characters in crosses between two varieties of the common flax (*Linum usitatissimum*) and between these and *L. crepitans* and *L. angustifolium*. She has dealt quantitatively with the length of seeds, length and breadth of petals, color of the flowers, degree of opening of the mature capsules, and the hairiness of the dissepiments of the capsules. Hairiness of the capsules and the lightest blue color of the flowers are each determined by a single Mendelian gene, but all the other characters are obviously more complex. The author believes that all of these characters are likewise determined by genes which segregate normally in the F_2, though they cannot be followed individually because several genes affect the same characteristic and act together in such a way that the grade of development of the character depends approximately on the number of these genes present. This results in a continuous series of gradations which are superficially indistinguishable from fluctuations, but which differ by being inheritable. Several evidences for the correctness of this interpretation are reported: The F_1 is in each case intermediate between the parents and no more variable than they; in the F_2 the variability is considerably increased, and the curves stretch out toward those of either parent, but frequently fail to reach them owing to the small size of the families investigated; when F_3 families are grown from the extreme variants of the F_2, a still closer approach to one or the other P_1 results, apparent identity with the parental type being attained in several cases. From the proportion of F_2 and F_3 families which approached in any given characteristic the condition of the P_1 generation, Miss TAMMES estimates the number of genes probably involved in differentiating the two parental types in each cross with respect to the several characteristics studied. She concludes that in length of seeds not less than four differentiating genes were involved in every cross made, in some crosses certainly a still larger number. In width of petals the simplest cross must have had differences between the parents in 3 or 4 genes, and the other crosses a considerably higher number. In flower-color different intensities of blue were apparently dependent on three genes. Between capsules which remain closed at maturity and those that spring wide open, 3 or 4 genes are involved. Later generations will be needed fully to test these conclusions.—GEO. H. SHULL.

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[34] TAMMES, T., Das Verhalten fluktuierend variierender Merkmale bei der Bastardierung. Recueil Trav. Bot. Neerlandais **8**:201–288. *pls. 3–5.* 1911.

Beach vegetation.—A detailed ecological study of the beach vegetation of that portion of the shores of Lake Michigan which extends from Waukegan, Illinois, to Kenosha, Wisconsin, has recently been made by GATES.[35] Unfortunately it contains little in the way of quantitative data upon the various factors involved, but as a record of the vegetation of this region it is an admirable and valuable contribution.

The lack of any definitely fixed conception of what constitutes the unit of vegetation known as a "plant association" is shown not only by the author's review of the literature upon the subject, but also by his subdivision of the vegetation of the very limited area under investigation into more than fifty different associations. Such a multiplication of associations indicates a danger of making the segregation upon a floristic rather than an ecological basis, and also points to the need of some well recognized subdivision of the association, and yet, even with the most conservative treatment, it is to be expected that a region such as this, representing as it does the meeting place of the northern conifer, the eastern deciduous, and the prairie plant provinces, would present an unusual number of vegetational types. The genetic relationship of these various associations is clearly indicated and exhaustive lists of species are given.—GEO. D. FULLER.

The black oaks.—At the meeting of the American Philosophical Society (Philadelphia) on April 19, 1912, Dr. TRELEASE discussed the classification of the black oaks. The abstract of his paper is as follows: Attention to bud and fruit characters has led to a classification of the black oaks quite different from their usual arrangement according to leaf-form, and five groups of species are recognized, three of the Eastern states, one of the Southwest, and one of the Pacific states. The eastern groups are the black oaks (black jack, turkey oak, Spanish oak, and quercitron), scarlet oaks (scarlet oak, gray oak, Hill's oak, red oak, Texas red oak, and bear oak), and swamp oaks, these of two sets, the water oaks (water oak, pin oak, and Stone Mountain oak) and willow oaks (shingle oak, willow oak, laurel oak, running oak, cinnamon oak, and myrtle oak). The Southwestern olive oaks (Emory's oak and the white-leaf oak) and the Californian holly oaks (evergreen oak, Highland oak, and Kellogg's oak) are less related to one another and to the eastern black oaks than these are to one another, and appear to have originated independently of them.

Nuclear phenomena in the Uredineae.—WEIR[36] has published a brief summary of the outstanding features of the Uredineae, which will be of service to those who wish a condensed outline of the nuclear conditions in the various stages of the life history of rusts.—J. M. C.

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[35] GATES, FRANK C., The vegetation of the beach area in northeastern Illinois and southeastern Wisconsin. Illinois State Lab. Nat. Hist. **9**: 255–272. *pls. 37–56.* 1912.

[36] WEIR, JAMES R., A short review of the general characteristics and cytological phenomena of the Uredineae, with notes on a variation in the promycelium of *Coleosporium Pulsatillae* (Str.). New Phytol. **11**: 129–139. 1912.

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THE DEVELOPMENT OF BLASTOCLADIA STRANGULATA, N. SP.[1]

J. T. BARRETT

(WITH PLATES XVIII–XX)

The genus *Blastocladia* was founded and incompletely described in 1876 by REINSCH (6) on the single species *B. Pringsheimii*, which for twenty years remained its sole representative. In 1896 THAXTER (9) rediscovered and made a careful study of the plant, which up to that time, apparently, had not been again observed. His studies cleared up several doubtful or unknown points in connection with its life-history and development, and led to the description of a new species, *B. ramosa*. Up to the present, so far as the writer is aware, no other species has been added to the genus. Aside from its peculiar characters, the genus is of particular interest because of its doubtful systematic position. Because of the resemblance of the resting spores to the deciduous conidia of certain *Pythium* species, THAXTER (9) placed the genus provisionally among the Pythiaceae. FISCHER (1) considers it with the genera which are doubtful or to be excluded from the Saprolegniaceae, while SCHRÖTER (7) includes it with the Leptomitaceae.

The species described in this paper fixes with considerable certainty, the writer believes, the true systematic position of the genus and is therefore described in detail.

This study was undertaken in the Botanical Laboratory of Cornell University under the supervision of Professor GEORGE F.

[1] Contribution from the Department of Botany, Cornell University. No. 140.

ATKINSON, to whom I wish to express my thanks for his advice and kindly criticisms.

Material and methods

A single plant of this species was discovered growing on an aphid which had accidentally fallen into one of several water cultures prepared for the purpose of entrapping various Phycomycetes. The specific culture referred to was made from soil and decaying vegetation taken from the bottom of a small almost dry inland pond in the vicinity of Ithaca. When first observed the plant bore large numbers of resting sporangia, whose arrangement and bright orange color gave it a very beautiful appearance. After washing through several changes of sterile water, the plant was placed in a solid watch glass for further observation. On examination the following day it was found that a number of zoosporangia had developed, a few of which had already discharged the characteristic zoospores first described by THAXTER (**9**) for *B. Pringsheimii*.

Cultures were immediately started with aphids and other animal tissue, from which an abundance of material in all stages of development was secured. After making several unsuccessful attempts, a pure culture of the organism was obtained in the following manner: A few nearly mature zoosporangia were cut from a plant, carefully washed until practically free from contamination, and allowed to discharge their zoospores in sterile water. By means of a platinum loop the water containing the zoospores was spread over the surface of newly prepared slants of sweet corn agar. In a few days the small plants appeared as more or less isolated refractive specks on the surface of the agar, and were easily lifted out with a sterile needle and transferred to new tubes.

Material for sectioning was obtained in various stages of development from both water and agar cultures. It was soon found that the latter yielded just as good and more easily handled material than the former and it was therefore more frequently used. To secure the best results with the latter method, plants bearing nearly mature zoosporangia were transferred to the middle of a poured plate of either potato or sweet corn agar, preferably the latter, in a few drops of sterile water. After a few hours to one day large numbers of zoospores will have been discharged and can easily be

spread over the plate by rocking the same or by the use of a sterile platinum loop. Thus distributed, the zoospores soon germinate and produce large numbers of usually simple plants bearing the reproductive organs. They commonly lie sufficiently close so that most of the agar may be cut out and fixed for microscopic study.

Three different killing solutions were used, which gave various results. These were medium chrom-acetic acid, Flemming's weak solution, and Gilson's fixer. After dehydration in the grades of alcohol or by evaporating down from 10 per cent glycerine, the material was cleared in cedar oil and imbedded in paraffin. Sections were cut 2–5 μ thick and stained on the slide.

The stains used were Flemming's triple stain with the orange G dissolved in clove oil, Heidenhain's iron-alum hematoxylin, and Gram's stain. The triple stain following Flemming's weak solution gave the best material for the study of the walls of the resting sporangia, papillae of dehiscence, and for fragmentation of the protoplasm to form zoospores; while Heidenhain's hematoxylin, when preceded by medium chrom-acetic acid, gave much the best material for the study of the protoplasm and nuclei. Gram's stain proved very good as a nuclear stain.

Description of the plant

The plant consists of a basal cell or cylinder whose lower extremity is attached to the substratum by a system of rhizoids, and supports above a dichotomously or umbellately branched system whose final branchlets terminate in one or more reproductive bodies (figs. 12, 58). At the points of origin of the branches, and occasionally elsewhere, there are more or less well marked constrictions of the mycelium. This character at once suggests a relationship to the members of the Leptomitaceae. The constrictions, however, are more abrupt and usually of less depth than those of that family. They mark off the plant into definite segments which are fairly constant in diameter throughout, although they occasionally have a tendency to enlarge slightly at one or both ends. This is especially noticeable in those branches which give rise to more than two branchlets. In this they resemble somewhat the branchlets of *Rhipidium americanum* Thaxter (10).

At the constricted points one finds pseudo-septa in various stages of development. These peculiar structures are unlike anything in the way of septa that I have seen described. In the older parts of the plant they reach their most perfect development, and then only incompletely separate the protoplasm of the adjacent segments. In a single well developed plant of some age, one may find the pseudo-septa in all stages of formation. They are first seen as separate processes or thickenings protruding inwardly from the wall at the constrictions. These processes increase in length, probably by accretion, until on meeting at the center of the cell, a fusion takes place and a definite central plate results.

Fig. 18, *a–d*, represents different stages of development of a septum, while figs. 19, 20, and 21 represent sections through such a stage as that shown in fig. 18, *a*. In fig. 19 the section is through one arm and the central plate, fig. 20 through two opposite radial arms and the central plate, while fig. 21 shows a section through the central plate alone. These pseudo-septa are much more highly differentiated than the "cellulin" rings which are present in *Gonapodya* and other Leptomitaceae. They permit a free interchange of the protoplasm, and only under conditions of injury to the hypha do they entirely close the lumen. Both the mycelial walls and the pseudo-septa fail to give any definite reaction for cellulose. After treatment with iodine and sulphuric acid, very rarely a slight trace of blue color is seen in the mycelial walls. The pseudo-septa become much swollen and take on a deep orange color, resembling in this respect the reaction secured by PRINGSHEIM (**5**) for the "cellulin granules."

In young actively growing plants the protoplasm is much vacuolated, granular, and contains, distributed throughout it, prominent nuclei containing deeply staining bodies (figs. 28, 32). Aside from the nuclei, there occur other deeply staining bodies which are more or less regular in form and of various sizes. They are very probably similar to those described by REINSCH (**6**) as independent, endogenously produced cells, which he was inclined to believe were the origin of the reproductive organs (see figs. 12, 28, 32). THAXTER (**9**) observed these same bodies in *B. Pringsheimii*, and saw no reason for assuming that they were other than

masses of fatty protoplasm. Their true nature has not been determined, but, as will be shown later, they have at least one definite function in connection with zoospore formation. They are always present in more or less abundance, their extent of occurrence depending, to a degree at least, on growth conditions of the plant. In old plants, especially when the production of reproductive bodies has ceased, large groups of such bodies may be seen collected near the pseudo-septa, and frequently elsewhere in the mycelium.

Bodies somewhat similar in appearance are known to occur in the hyphae of members of the Saprolegniaceae. PRINGSHEIM (**5**) describes these at length and records a series of microchemical tests to determine their nature. According to his conclusions they are neither a proteid nor a carbohydrate substance, but rather waste products of metabolism.

Under favorable conditions of growth, a branchlet when terminated by a reproductive body may continue its growth by the production of a sub-branch (fig. 32). This sub-branch may be likewise terminated, sooner or later, and continued growth repeated as before. The length and rapidity of growth of these sub-branches determines whether the reproductive bodies shall occur at intervals or in a more or less compact head or group (figs. 6, 7, 12). This type of sympodial branching occurs in depauperate specimens of *Rhipidium americanum* (THAXTER **10**). It has also been noted for *Apodachlya*.

Under the best normal conditions for growth, the production of zoosporangia precedes that of resting sporangia. In pure cultures this order is easily reversed by properly manipulating external conditions. In a frequently refreshed culture, zoosporangia alone are at first produced, while on the other hand plants in a culture started and maintained in a small amount of water usually give rise to resting sporangia only.

The extent to which branching may proceed before the production of reproductive organs varies greatly. This may continue until a well formed almost hemispherical tuft is produced, or on the other hand zoosporangia may develop soon after the germination of the zoospore on the terminal end of the more or less

elongated basal cell. This condition occurs particularly on young plants started on agar and subsequently transferred to water. If sufficient moisture is present the same thing may take place directly on the agar (figs. 4, 5). Zoosporangia may be produced singly or in chains (fig. 59).

The growth of the plant is rapid when the best external conditions are offered. Observations made relative to this point showed that in one case hyphae which were just emerging from the body of an aphid at 10:30 A.M. had produced at 5:30 P.M. of the same day mature zoosporangia, some of which were discharging zoospores. The size of individual plants varies greatly with the purity of the cultures and the nature and amount of nutrient material at hand.

Development of zoosporangia

The zoosporangia are broadly oval to almost spherical, rarely elliptical, smooth, hyaline, and fairly constant in form and size. They may originate terminally or subterminally on the branchlets. In the former case the first indication of such a development is a slight swelling of the hyphal end accompanied by a well marked change in the protoplasm (fig. 11, *a–c*). Before reaching its normal size, the zoosporangium becomes cut off from the hypha by a septum, and papillae of dehiscence begin to appear. When produced subterminally, the mature zoosporangium may be borne on a more or less elongated branchlet, as previously noted, which originated from the parent branch directly below another reproductive body (fig. 6), may be sessile (fig. 12, *b*), or even develop as swollen segments cut off by septa (fig. 12, *a*). The latter method when continued produces a chain of zoosporangia (fig. 59). As a result of cutting off the ends of fertile branches, zoosporangia may bud out from the remaining parts in various places. In certain instances the contents of the injured branches give rise to zoospores without any modification in form.

The zoosporangia of *B. Pringsheimii*, after discharging their zoospores, drop from the plant, leaving numerous scars. This was noted by THAXTER (**9**) and also by PETERSEN (**4**). I have never observed this phenomenon to take place in *B. strangulata*. Old

empty zoosporangia may be seen still attached to the plants weeks after they have ceased to produce reproductive organs.

As growth of the zoosporangium proceeds, there is a noticeable condensation of the protoplasm in the center, around which can be seen a number of indistinct vacuoles of irregular shape. There is little apparent change from this condition until the zoosporangium has reached its maximum size. The contents then become coarsely granular and no vacuoles are apparent. This stage may persist for some time if conditions for further development become poor. In fact, it is in this stage that zoosporangia rest at times for days. Suddenly the coarse granular character changes to one with fine evenly distributed granules, and the whole contents assume a much lighter appearance. After 15–30 minutes one can discern the formation of areas surrounded by faint granular but irregular lines. These become rapidly more prominent, and in a few minutes a slight movement can be detected within the zoosporangium. The areas represent the zoospores and their discharge is about to take place (fig. 8). The papillae of dehiscence, sometimes numbering as many as eight, become more and more extended and refractive until one or more finally break open, permitting the zoospores to escape. They pass out in single file, at first rather rapidly, then more slowly as the pressure within the zoosporangium becomes lessened (fig. 56). Being of a plastic nature, they squeeze through the opening, arriving at the outside irregular in form, and very commonly with their cilium held in the opening by the next emerging zoospore. After a few seconds they move slowly away, assuming their normal form.

The zoospores are oval to elliptical, not infrequently slightly ovate, in which case the narrower end is the anterior one. The number of cilia varies from one to three, and they are attached at the posterior end. From a large number of careful examinations of both living and stained preparations of zoospores, I assume that the uniciliated condition is the typical one, as it occurs much more frequently than the other two types. The triciliated zoospore is rarely seen, while the biciliated form is common. The zoospores of *B. Pringsheimii* possess, according to THAXTER (**9**), one or two

cilia. He considered the latter number the typical one, while PETERSEN (4) has described the zoospores as uniciliate.

The zoospore contains a large subtriangular centrally located body which resembles a large nucleus (fig. 23). THAXTER observed this body and described it as follows: "The nucleus is very large and subtriangular in outline, its base connected with that of the cilia by a fine strand of protoplasm." Fig. 24 shows very distinctly the connection of the cilium with the base of the large central body. The zoospore was killed with a 1 per cent solution of osmic acid and stained with an alcoholic solution of Magdala red. In the process the outer portion of the zoospore broke away, leaving the cilium still attached to the central body as represented. There can be observed in properly killed and frequently in living zoospores a more or less hyaline globule situated at the base of the central body, which contains a highly refractive granule. This body is undoubtedly the nucleus of the zoospore and will be more fully discussed later. The zoospore also contains groups of large and small granules, evidently of a fatty nature, which are principally located in front and to the rear of the so-called central body.

In movement the zoospores proceed in a more or less direct course, with a slight swaying of the body, and at times accompanied by a slow rotation on the longitudinal axis. If supplied with sufficient oxygen they may continue to swim for a number of hours, but when mounted on a slide under a cover glass, where the oxygen supply is small, they soon cease movement and germinate.

Fig. 28 shows a section of a young reproductive body, presumably a young sporangium, stained with iron-alum hematoxylin. The protoplasm is granular, vacuolated, and contains distributed throughout it prominent nuclei and large and small deeply staining bodies to which reference has already been made. The number of nuclei is at first small, and there is apparently no marked passage of the nuclei from the adjacent portions of the mycelium such as occurs in the developing sporangia and sexual organs of many other Phycomycetes. The nuclei in the upper half of the sporangium are in various stages of division. This condition may be found in young rapidly growing hyphae and principally at the growing point. As growth proceeds the number of nuclei rapidly

increases, until 40–70 are produced, usually about 60 in average-sized sporangia. About the time the zoosporangium reaches its full size the nuclei arrange themselves about the periphery. A large number of the sections show this condition, which seems to indicate that the zoosporangia rest in this stage. This condition probably agrees with that described above for the living specimen in which the protoplasm is coarsely granular.

Fig. 29 represents a section of a zoosporangium which is entering the stage of zoospore formation. The large nuclei have become distributed throughout the more coarsely granular protoplasm. The number and size of the deeply staining bodies has increased, while some of them show a vacuolate condition. On some of the nuclei can be seen deeply staining masses of small size. Other nuclei are associating themselves, more or less closely, with some of the larger masses.

This condition is carried still farther in fig. 30. In a number of cases the nuclei are more or less imbedded in the deeply stained bodies, in others they are still free from them. These stages very probably correspond to the more or less homogeneous stage of the living zoosporangium which just precedes the differentiation of the zoospores. Fig. 30 also shows the beginning of segmentation of the protoplasm. It proceeds from the periphery inward in a more or less radial direction, much as described by HARPER (**2**) for *Synchytrium decipiens*. The lines of division are first recognized as rows of granules, at first more or less indefinite, but which become more and more apparent until they are seen entirely to outline the spore mass.

Fig. 31 represents a part of a section of a sporangium in which segmentation is almost complete. The limiting surfaces of the spore masses in a number of cases have separated. Apparently contraction has taken place, which would indicate that the mature zoospores occupy less space than the original masses of protoplasm from which they are formed. HARPER (**2**) observed that shrinkage of the protoplasm takes place in the early stages of cleavage in *Synchytrium decipiens*, and suggested a loss of water as the cause. He also observed the open spaces formed by the separation of the segmented masses.

It will be observed (fig. 31) that the nuclei with their associated material have assumed a more regular form. The nucleus itself is drawn out to a point which, in some cases, extends to the very limits of the spore. No indications of cilia have been observed at this stage, but they can be seen occasionally in a later stage, that is, at the time of discharge of the zoospores. The condition of the nucleus described strongly suggests that the cilia have their origin through its direct influence.

Segmentation usually results in the formation of uninucleate zoospores. Occasionally, however, one may find binucleate zoospores with the nuclei in the same or different central bodies, or what I shall hereafter call food masses or bodies. Fig. 34 shows normal zoospores ready to escape from the zoosporangium. Fig. 35 shows the two types of binucleate zoospores of the same age as those in fig. 34.

In preparation for germination the zoospore comes to rest, takes on a spherical form, and gradually absorbs its cilium, which in the process commonly becomes enlarged at the end (fig. 25). The large reserve food body disappears and a large number of variously sized granules take its place. In the course of 10–20 minutes the germ tube makes its appearance and grows rapidly, forming the basis for the subsequently developed rhizoid system (figs. 26, 27, 2, *a–c*). The body of the zoospore forms the basal cell of the plant.

Fig. 36 represents a zoospore stained with iron-alum hematoxylin, preparing to germinate. As described above, the reserve food mass has apparently broken up into a number of deeply staining granules. As the germ tube elongates, the nucleus increases in size (fig. 38) and finally divides to form two (fig. 39). Accompanying the rapid growth of the young plant the protoplasm becomes more and more vacuolated and finally granular (fig. 40). Stained preparations of germinating zoospores beyond the four-nucleate stage were not obtained.

Just what the nature of the so-called reserve food bodies is has not been determined. Fig. 41 shows a zoospore killed with iodine solution. The nucleus and some granules show distinctly, while the large food body in most cases is invisible. Fig. 42, killed with weak Flemming solution, reveals that body clearly, and also the

blackened condition of the granules, which indicates their fatty nature.

Papillae of dehiscence occur on the zoosporangia of many Phycomycetes. In most cases they have been described as small swollen areas in the sporangial wall, or tips of exit tubes which become gelatinized and allow the emission of the zoospores to take place. An interesting condition is found in *Rhipidium americanum*. The zoosporangium possesses a double wall; the outer forms a cap over the papillae, which, on the discharge of the zoospores, becomes lifted up by the protruding inner wall; the latter forms a cylinder or vesicle which incloses the discharging zoospores; it ruptures immediately, setting them free (THAXTER 10). A similar condition prevails for *Sapromyces*.

So far as I have been able to learn, the structure and behavior of the papillae of *B. strangulata* differ from anything yet described. In the living sporangium the papilla possesses what appears to be an outer highly refractive hyaline convex cap, with a less refractive area between it and the protoplasm of the sporangium. The external part becomes more and more convex as gelatinization proceeds (fig. 8). Just before the disappearance of the outer part it loses its high refractive power to some extent, and has the semblance of glycerine. Suddenly the thin ungelatinized portion of the wall breaks, and becomes forced out, leaving a ragged rim, many times, about the opening. The adjacent gelatinized part is immediately dissolved in the surrounding water, and to all appearances the exit pore is open. In a few seconds the zoospores begin to escape. Under what seem to be normal conditions, a vesicle is formed which incloses at least a part of the zoospores on their discharge. This vesicle soon breaks and the zoospores are set free (fig. 13). Frequently no such vesicle can be seen, and in such cases the zoospores escape as shown in fig. 14. The formation of such an inclosing membrane immediately suggested a double wall to the zoosporangium, and also that it was the inner of the two which either protruded as in *Rhipidium americanum*, or that by its gelatinization it was enabled to stretch out in the form of a thin sac.

On the examination of sections it was found that neither assump-

tion was correct. Fig. 9 shows a section through an immature papilla and the adjacent wall of the zoosporangium. It is very evident that the wall is single, but that there are two distinct parts to the gelatinized plug of the papilla. The plug has a strong affinity for stain, especially safranin. The ungelatinized part of the wall is seen as a thin unstained layer extending over the convex plug. The wall immediately surrounding the papilla is thickened so as to form a sort of collar. This is clearly seen in empty sporangia. Fig. 10 shows the two parts of the plug separated as a result of cutting the section. It will be seen that the inner portion bears a close relation to the protoplasm. Such a section is common. In those sections which show a contraction of the protoplasm from the wall of the zoosporangium, almost invariably it is found to adhere closely to the inner part of the plug, whether that remains in place or not. It is this part of the plug that has the less refractive power in the living state and that on stretching out forms the vesicle referred to above. Very probably gelatinization is brought about by the action of an enzyme secreted by the protoplasm in the region about the papilla, which may account for the close relation between the two just described. Apparently the outer part of the plug becomes more thoroughly gelatinized than the inner, while the outer thin unstained part of the wall over the papilla is little or not at all affected.

This condition may be explained, it seems, by assuming that the wall of the zoosporangium is made up of lamellae which differ slightly in composition and which are differently affected by the gelatinizing agent. This assumption is strengthened by the fact that in a few sections the condition illustrated in fig. 9 was observed, that is, the line separating the two portions of the gelatinized plug extended slightly into the sporangial wall.

Development of resting sporangia

The resting sporangia agree in general to similar bodies described by REINSCH (6) and THAXTER (9) for *B. Pringsheimii*, and by THAXTER (9) for *B. ramosa*. In *B. Pringsheimii* they are called resting spores by THAXTER, and are considered as doubtful oospores by REINSCH. They are indicative of the older condition of the

plant, and when mature are deciduous. According to THAXTER, the mature resting spore is surrounded by two walls, an outer, thin and smooth, and an inner, thick and apparently perforated or pitted. He did not study a section of the wall, hence was not able to determine the structure definitely. They possess several large oil globules, are oval to pyriform, and vary in form almost as much as the zoosporangia.

In *B. ramosa* the resting sporangia, or spores, are "bluntly rounded, gradually narrower toward a truncate base, and about 30×11 μ." In this species the resting spores are less variable in form than those of *B. Pringsheimii*, but vary somewhat in size. The walls are very little thicker than those of the sporangia. Resting spores of neither species were seen to discharge zoospores or to germinate.

The resting sporangia of *B. strangulata*, for such they are, as will be shown later, are very constant in form and vary only slightly in size. They are ovate in form, with the narrower basal end truncate (fig. 15). As previously noted, they occur at almost any age of the plant, depending on the conditions of growth, and remain attached at maturity. They have their origin, in general, in the same manner as the zoosporangia, and in the younger stages cannot be distinguished from them. The wall begins to thicken early, and this, together with the absence of papillae, indicates that resting sporangia are developing. When they are mature they possess three walls, an outer and an inner, thin, smooth, and hyaline, and a middle, thick, perforated, and orange colored. The peculiar perforated nature of the middle layer can easily be made out in sections of mature resting sporangia. The pores are conical in shape, with the broad end outward. The greatest diameter is 0.8 μ and the least 0.3 μ. Fig. 16 shows a surface view, while fig. 17 is a diagrammatic representation of a cross-section, showing the pores and the inner and outer walls. The pores are more or less regularly arranged in rows, as seen in fig. 15.

The mature resting sporangia contain a number of oil globules which are not strikingly noticeable as they are in many other resting bodies of a similar nature. In describing these bodies for *B. Pringsheimii*, PETERSEN (4) says: "Peculiar pointed or rounded

cylindrical resting spores with a flat base and remarkably porous walls, without much content, appear in place of the zoosporangia."

In the young stages the protoplasm has much the same appearance as that of the young sporangia. Fig. 32 represents a section of a developing resting sporangium in which the nuclei are arranged about the periphery. The central mass of granular protoplasm, containing several reserve food bodies, is surrounded by prominent vacuoles. In the mature sporangium the protoplasm forms a definite regularly arranged network in which the nuclei are distributed (fig. 33). There are present, also, deeply staining masses, more or less irregular in shape, which probably represent the fusion of several reserve food bodies.

On germination the contents of the resting sporangia escape in the form of zoospores not unlike those formed in the zoosporangia. According to all observations and tests made, it is necessary that the resting sporangia pass through a period of rest before germination. I have not found any to germinate that were not at least one month old. This applies to culturés developed both in water and on agar. On the transference of the sporangia to fresh water there is no apparent change for some time. After 18–20 hours the two outer walls become cracked open, due very probably to the absorption of water. Sometimes they crack in several places, bringing to view the inner hyaline wall which bears one or more papillae of dehiscence. In a short time the normal discharge of zoospores takes place (fig. 22).

Nuclear division

The resting nuclei are usually spherical in form and contain a large deeply staining body which I assume to be a chromatic nucleolus. Surrounding this body is a fine granular cytoplasm which can be seen forming an irregular network (fig. 43). They vary in size from very small, almost invisible dots, to those with a diameter of 6–7 μ. The smaller are found in the actively growing parts where nuclear division more commonly takes place. The mode of division is rather unusual and suggests a form of amitosis. The first indication of such a nuclear division is a change of the chromatin mass from the more or less normal spherical to an elongated form (figs. 48, 52). A transverse line of division is next

seen (fig. 47). The two parts then round up (figs. 45, 53), separate (figs. 49, 51), and appear as two large nucleoli. A wall is finally laid down between the daughter chromatin masses, and the two nuclei result (figs. 44, 55). Frequently nuclei may contain three of these bodies (fig. 50). Evidently one of the two daughter masses of the first division divided before any nuclear wall separated them.

In dividing nuclei stained with iron-alum hematoxylin, there is a faintly staining homogeneous substance connecting the separating chromatin masses, which suggests some sort of a spindle. Two explanations suggest themselves: (1) that we are dealing with direct nuclear division and that the faintly staining substance is the cytoplasm contracted about the dividing chromatin masses; and (2) that division is indirect and that the large chromatin mass represents a single chromosome.

It seems unusual, if not improbable, that such a highly differentiated plant in so many respects should possess only a direct method of nuclear division. The fact, however, that no sexual organs are known for any of the species of the genus may have some bearing on the question. HUMPHREY (**3**) found a very similar nuclear division to take place in the hyphae of *Achlya apiculata*. From all observations yet made, I am inclined to hold to the view that we are dealing with a peculiar type of mitotic division. Further studies concerning the question are contemplated.

Since the species appears to be a new one, I add here a description giving the more important characters as observed by the writer.

Blastocladia strangulata, nov. sp.—Main axis oval to cylindrical, divided at the base into a number of rhizoidal divisions; above giving rise to a one to several times dichotomously or umbellately branched system whose ultimate branchlets produce terminally or subterminally zoosporangia and resting sporangia; definite constrictions and perforated pseudo-septa at the points of branching. Zoosporangia, oval to nearly spherical (50–63×40–52 μ), possess several papillae of dehiscence, and produce a comparatively small number of rather large zoospores. Zoospores 12×8 μ, with one to three cilia, usually one. Resting sporangia ovate to nearly oval, with a truncate base, 45×35 μ; the wall consists of

three layers, the middle thick, perforated, and orange colored; on germination giving rise to zoospores. Whole plant 200–2000 μ high, its main axis 40–100 μ in diameter.

Found but once, and on an aphid in a water culture made from soil taken from the bottom of an almost dry inland pond near Ithaca, N.Y.[2]

Axi primario ovato ad cylindricum, basi divisionibus rhizomatoideis numerosis, sursum copiose dichotome v. subdichotome ramoso; ramosis intervallis constrictis; pseudo-septis perforatis intra ramulorum basim formatis; zoosporangiis ovalibus ad sphaeroidea, 50–63×40–52 μ, papillas dehiscentes paucas ferentibus; zoosporis ovalibus, 12×8 μ, cilio plerumque simplici ornatis; sporangiis perdurantibus, rotundatis, basim versus graditim angustioribus et truncatis, 45×35 μ, zoosporis foventibus.

Hab. Ad aphid in aqua, Ithaca, N.Y.

Summary

1. The plant resembles in general the other species of the genus. Its mycelium is definitely constricted, which fact, it seems, definitely places the genus in the family Leptomitaceae.

2. It possesses peculiar perforated pseudo-septa which are formed at the constrictions, and which in a way are comparable to the "cellulin rings" of other members of the Leptomitaceae.

3. Zoosporangia are provided with a number of papillae of dehiscence distributed over the surface, which are formed as the result of the gelatinization of small circular areas of the wall. The resulting plug is made up of two distinct parts, the inner of which forms a vesicle into which the zoospores escape at the time of their discharge.

4. The zoospores possess a large centrally located subtriangular mass of apparently some reserve food substance, probably proteid in nature, at whose base is located the nucleus. They are typically uniciliated, with the cilium in direct relation to the nucleus.

5. Resting sporangia possess a three-layered wall; the outer and inner layers thin and hyaline; and the middle thick, perforated, and orange colored. After a period of rest of several weeks, germination takes place by the formation of zoospores.

[2] During May and June 1911 this species appeared several times in water cultures made from two garden soils one-fourth mile apart near Urbana, Ill. As it was found in soil collections made at different times and parts of the gardens, it was evidently not rare in those particular locations.

6. On germination the zoospore produces a germ tube which forms the basis of the rhizoid system, while the body of the spore becomes the basal cell of the plant.

7. Nuclear division is somewhat unusual, apparently, and reminds one of amitosis. It seems to the writer, however, that it is more probably a form of mitotic division dealing with a single large chromosome.

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EXPLANATION OF PLATES XVIII–XX

FIG. 1.—Biciliated zoospore.

FIG. 2.—Different stages in the germination of the zoospore.

FIG. 3.—Young plant with basal cell showing rhizoids and two branches which are beginning to branch dichotomously.

FIG. 4.—Young plant started on potato agar and subsequently transferred to water where sporangial development took place.

FIG. 5.—Plant similar to the one shown in fig. 4, with an empty sporangium and another almost mature below it.

FIG. 6.—A branch with sympodial arrangement of resting sporangia.

FIG. 7.—Resting sporangia more closely arranged on the branchlet, a more frequent condition in old cultures.

FIG. 8.—A mature sporangium showing zoospores differentiated and two papillae of dehiscence.

FIG. 9.—A stained section of a papilla of dehiscence.

FIG. 10.—Another section of a papilla of dehiscence, showing the protoplasm and attached inner portion of the plug drawn away from the wall.

FIG. 11.—Early stages in the development of zoosporangia.

FIG. 12.—A mature plant, showing the rhizoid system, manner of branching, and arrangement of reproductive bodies.

FIG. 13.—A mature sporangium discharging its zoospores into a thin vesicle which soon ruptures.

FIG. 14.—A mature zoosporangium discharging its zoospores without the formation of a vesicle.

FIG. 15.—Resting sporangium, showing the relative position of the pores in the much thickened wall.

FIG. 16.—An enlarged portion of the surface of a resting sporangium.

FIG. 17.—A diagrammatic representation of a microscopic section of the wall of a resting sporangium.

FIG. 18.—Different stages in the development of the pseudo-septa located at definite constrictions in the hyphae.

FIGS. 19–21.—Microscopic sections through such a septum as shown in fig. 18, *a*, giving the various appearances that result.

FIG. 22.—Germinating resting sporangium: outer walls cracked open, exposing the inner thin wall bearing papillae of dehiscence.

FIG. 23.—A zoospore showing the nucleus with its accompanying mass of reserve food material, and two cilia.

FIG. 24.—Zoospore killed with a 1 per cent solution of osmic acid and stained with Magdala red; the outer portion of the zoospore broke away, leaving the reserve material and nucleus with the single cilium attached.

FIG. 25.—Zoospore coming to rest preparatory to germination; contraction of the cilium taking place and contents becoming granular.

FIGS. 26, 27.—Early stages in germination of the zoospore: from living specimens.

FIG. 28.—Section of a young zoosporangium, showing nuclei in division and also several large deeply staining food bodies.

FIG. 29.—Section of a zoosporangium at the time of early nuclear association with the reserve food material preparatory to zoospore formation.

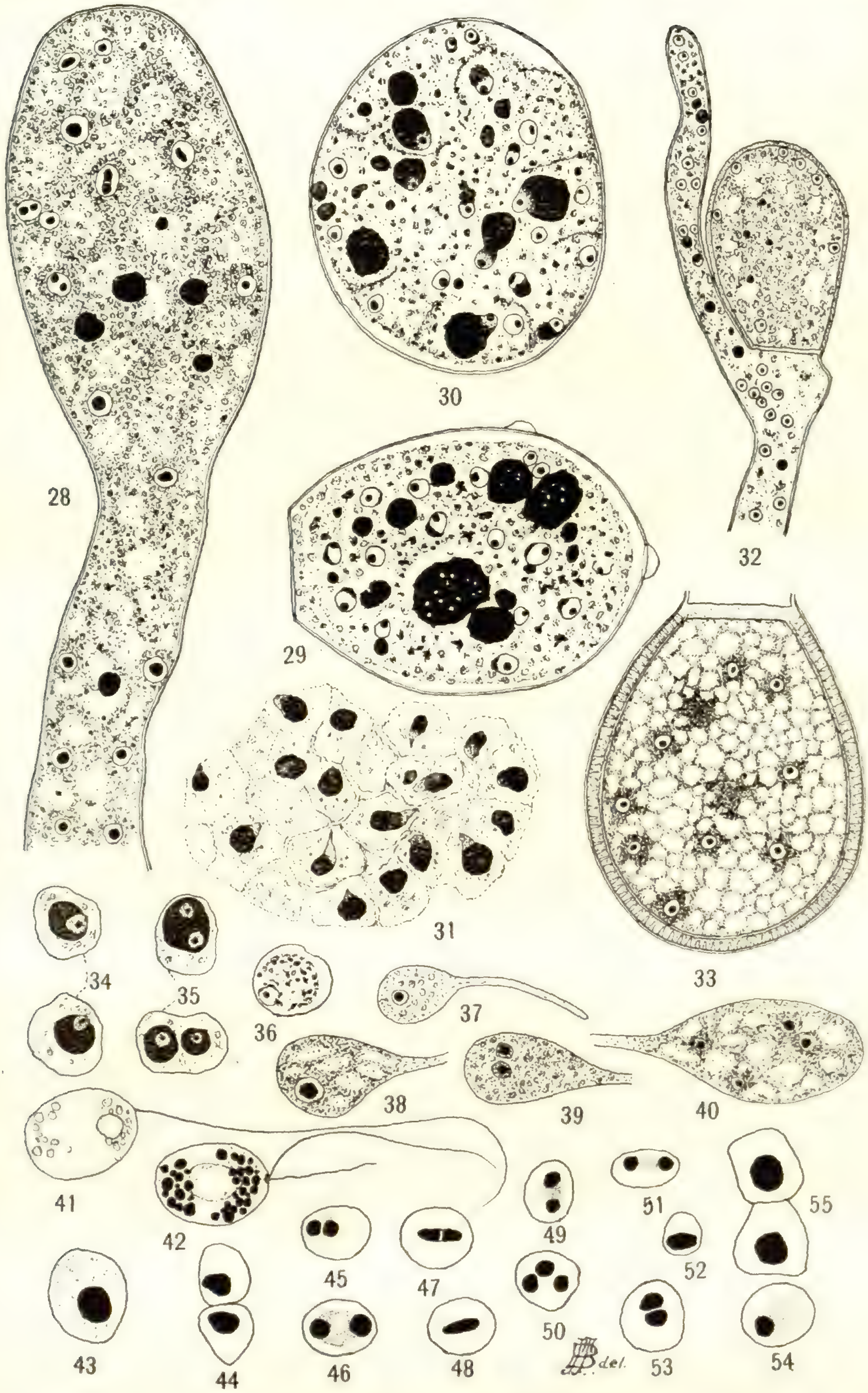
FIG. 30.—Later stage than that shown in fig. 29: many nuclei more or less imbedded in the reserve food material; lines of segmentation appearing at the periphery.

FIG. 31.—Section of a zoosporangium in which segmentation has taken place.

FIG. 32.—Section of a developing resting sporangium and a sub-branch.

FIG. 33.—Section of a mature resting sporangium.

BARRETT on BLASTOCLADIA



BARRETT on BLASTOCLADIA

56 57

58 59

BARRETT on BLASTOCLADIA

FIG. 34.—Stained zoospore from a ripe zoosporangium: nuclei very distinct; iron-alum hematoxylin.

FIG. 35.—Binucleate zoospores.

FIG. 36.—Zoospore preparing for germination: the large reserve food body is broken up into small granules.

FIG. 37.—Uninucleate germinating zoospores.

FIG. 38.—Germinating zoospore showing the large nucleus just previous to division.

FIG. 39.—Binucleate stage of a germinating zoospore.

FIG. 40.—More advanced condition of a germinating zoospore.

FIG. 41.—Zoospore killed with iodine: nucleus clearly shown, but the food body is invisible.

FIG. 42.—Zoospore killed with weak Flemming's solution: granules surrounding the nucleus and reserve food body stained black.

FIG. 43.—Resting nucleus, showing a large deeply staining chromatin mass surrounded by faintly staining cytoplasm.

FIG. 44.—Late stage in the division of a nucleus.

FIGS. 45–55.—Various stages of nuclear division.

FIG. 56.—A photomicrograph of zoosporangia discharging zoospores, and resting sporangia.

FIG. 57.—A photomicrograph of the plant from which fig. 56 was taken.

FIG. 58.—A photomicrograph of a small entire plant.

FIG. 59.—A photomicrograph of a young plant grown on agar, which shows the arrangement of zoosporangia in chains.

THE ORCHID EMBRYO SAC[1]

LESTER W. SHARP

(WITH PLATES XXI–XXIII)

During the spring of 1910 it was the writer's privilege to visit the island of Jamaica as one of a party of botanists from the Johns Hopkins University under the leadership of Professor D. S. JOHNSON. In view of the number of orchids available in the region visited, it was suggested by Professor JOHNSON that a study of the embryo sacs of these species, together with those of certain forms growing in the University's greenhouse at Baltimore, might for several reasons prove of value.

The orchids, standing at the end of a great evolutionary line, the monocotyledons, and reaching extreme specialization in other features, may be expected to show instructive deviations from the usual type of embryo sac, and it is through a study of such deviations that a final explanation of the origin and nature of the angiosperm embryo sac will probably be reached. They should also be most likely to reveal the end result in the reduction of the female gametophyte, which is seen occurring as one passes from the lower heterosporous groups to the higher. Furthermore, the data at hand on the orchid embryo sac, in part very suggestive, have been somewhat scattered, the details being well known in comparatively few forms, so that we have not known just what relation the cases reported bear to any general situation which may be present among orchids.

Although the number of additional species here described is small for a group as large as the Orchidaceae, they are well scattered throughout the family, so that taken together with species previously described they place us in a better position to draw conclusions on the general tendency of the group.

For the sake of clearness the different forms will be considered separately, and only two or three of them in detail.

[1] Botanical contribution from the Johns Hopkins University. No. 25.

Epidendrum variegatum Hook.

The course of development in this species corresponds in many respects very closely to that recently reported for *Epipactis pubescens* (BROWN and SHARP **2**), in which an 8-nucleate sac of the ordinary type is derived from one or less frequently from four megaspores. In *Epidendrum variegatum*, while the majority of sacs developed from one megaspore, the proportion of cases in which four are concerned is apparently greater than in *Epipactis*.

The archesporial cell, as in all of the other species examined, is hypodermal in position, and since it cuts off no parietals it is at the same time the megaspore mother cell. After passing through synapsis (fig. 1) and the other prophases preceding reduction, the nucleus of this cell divides. The position of the spindle and the wall formed upon its fibers is variable, which seems to be an important factor in determining the nature of the subsequent development. The spindle may be formed near the micropylar end of the mother cell, the resulting daughter cells in this case being very unequal in size, or the spindle may arise near the middle, the daughter cells then being approximately equal. Between these two positions of the spindle all gradations are found.

In the event of an unequal division the subsequent development is as follows. The small micropylar daughter cell at once begins to disorganize, while the large inner one divides (fig. 2) to form two megaspores. Of these the inner one only remains functional, the outer one disorganizing along with the micropylar daughter cell (fig. 3). The nucleus of the functioning megaspore divides without the formation of a wall (fig. 4) and the resulting nuclei again divide freely to form the 4-nucleate sac (fig. 5). At the next division (fig. 6) cell plates appear on the fibers of all four spindles, but those formed in connection with the chalazal nuclei usually disappear, so that the antipodals are in most cases represented by free nuclei.

When the division of the megaspore mother cell is equal (fig. 7), the cell plate which forms upon the spindle fibers is ephemeral and the two daughter nuclei are left free in the same cell cavity. Vacuolation occurs in the cytoplasm, usually in the region between the nuclei (fig. 8), but at times near the ends of the cell with the two nuclei at the center (fig. 9). At the division of these nuclei distinct

cell plates appear on the spindle fibers but do not persist, so that the four resulting nuclei remain free in the cytoplasm (figs. 10, 11). Since these have arisen by two successive divisions from the nucleus in which the heterotypic prophases occur, they are to be regarded as megaspore nuclei, and any one of them is thus the morphological equivalent of the nucleus shown in fig. 3. By one further division these four megaspore nuclei give rise to an 8-nucleate sac similar in all essential points to that derived from a single megaspore. An egg apparatus of the ordinary type is organized; the antipodal nuclei may or may not be separated by walls; and the two polar nuclei meet in the vicinity of the egg (fig. 12).

The various stages described in the foregoing paragraph may be distinguished from those in the development of a sac from a single megaspore by the absence of disorganized cells at the micropylar end. In later stages these latter become indistinguishable from the disorganized contents of the epidermal cells of the nucellus, so that it is then unsafe to use them as evidence, but there appears to be nothing against the assumption that the fate of the embryo sac is the same whether it has been derived from one megaspore or from four.

In this *Epidendrum*, as in *Epipactis*, two megaspores evidently take part in the formation of the embryo sac in a few cases. This condition results when the division of the megaspore mother cell is very unequal and that of the inner daughter cell equal, the separating wall at the second mitosis being ephemeral.

The pollen tube enters the sac, disorganizes the two synergids, and liberates two male nuclei. One of these fuses with the egg nucleus, while the other fuses with the two polars (fig. 13). The endosperm nucleus formed by the latter fusion undergoes no division, but degenerates along with the three antipodal nuclei (fig. 14).

The first few divisions of the fertilized egg are transverse, resulting in a filamentous proembryo of a varying number of cells. Longitudinal walls soon come in, and for a time the cells show a very regular two-ranked arrangement (fig. 15). Fig. 16 represents a proembryo of *E. verrucosum*, in which the number of transverse divisions has been very high, forming a filament of about 20 cells.

Figs. 17 and 18 show two stages in the development of the proembryo of *E. cochleatum*. In these three figures is seen the general course followed by the *Epidendrum* proembryo up to the stage found in the mature seed. Multiplication of cells commences at the chalazal end of the filament and extends upward, resulting in an oval mass of cells which is still to be regarded as a proembryo, since the body regions have not yet been marked out.

Epidendrum verrucosum Sw., **E. cochleatum** L., **and E. globosum** Jacq.

The embryo sacs of these forms were briefly examined. In the first two species stages were observed corresponding in all essential features to figs. 1, 3, 5, 12, and 14. In *E. globosum* were seen an ordinary 8-nucleate sac and a stage like that shown in fig. 14. It thus appears that *E. verrucosum*, *E. cochleatum*, and probably *E. globosum*, agree with *E. variegatum* in the formation of an embryo sac of the usual type from a single megaspore. The investigation of these three additional species was not carried far enough to determine whether they also show other methods of developing the embryo sac or not.

Phajus grandifolius Lour.

The early stages in the development of the embryo sac in this form correspond to those described above for those cases of *Epidendrum* in which but one megaspore is concerned in the formation of the sac.

The megaspore mother cell (fig. 19) divides unequally and the chalazal daughter cell again divides to form two megaspores. The outer daughter cell and megaspore disorganize (fig. 20), while the inner megaspore initiates the formation of the embryo sac. The nucleus of this functioning megaspore by two successive divisions gives rise to four; two of these lie at each end of the sac, the center of which is occupied by a large vacuole. The two chalazal nuclei undergo no further division, while those in the micropylar end divide to four (fig. 21), which become organized into an egg apparatus of the usual type and a free polar nucleus. This polar migrates toward the base of the sac and lies near the two chalazal

nuclei which have failed to divide (fig. 22). These three may fuse very soon (fig. 23) or they may remain distinct through the subsequent stages (fig. 24). In fig. 23 the egg apparatus fills an unusually large portion of the embryo sac.

The pollen tube discharges two male nuclei into the sac; one fuses with the egg nucleus and the other becomes associated with the free antipodal nuclei and micropylar polar (fig. 24). These latter nuclei show little regularity in behavior; they may begin to disorganize at any stage, but usually become more or less fused before this occurs. In any event no endosperm is formed.

The fertilized egg divides transversely to form a short filamentous proembryo, which attains a length of three or four cells before the first longitudinal division occurs. At this stage the cell toward the micropyle begins to elongate and push out into the surrounding placental tissue as a haustorial suspensor (figs. 25, 26). Later this dies away so that the proembryo in the mature seed is a simple rounded mass of cells (fig. 27).

Corallorhiza maculata Raf.

In *Corallorhiza* the embryo sac develops in a manner similar to that in *Phajus grandifolius*, as a comparison of figs. 28–33 (*Corallorhiza*) with figs. 20–24 (*Phajus*) will show. Consequently the above description of the sac of *Phajus* applies in all essential points to *Corallorhiza*, so that a separate account of the latter is unnecessary.

The proembryo of *Corallorhiza*, as described by LEAVITT (6), has a very long two-celled suspensor, which projects through the micropyle and enters the tissue of the placenta.

Broughtonia sanguinea R. Br.

This species shows the same peculiarity described above for *Phajus* and *Corallorhiza*. The innermost megaspore gives rise to a sac with six nuclei, the primary antipodal nucleus dividing only once. This division does not usually occur until the two nuclei in the micropylar end divide to four, so that three spindles are observed in the sac at one time.

Bletia Shepherdii Hook.

This form affords another example of the derivation of the female gametophyte either from one or from four megaspores, the course followed being apparently connected with the position of the wall formed at the division of the megaspore mother cell, as pointed out in *Epidendrum variegatum*. The nucleus of this cell goes into synapsis (fig. 34) and at its division the spindle may lie near the micropylar end of the cell or at its center. In the former case the daughter cells are very unequal in size; the small micropylar one degenerates, and the chalazal one divides to form two megaspores (fig. 35). Of these the outer one disorganizes, while the inner one enlarges and continues the development, by two successive divisions giving rise to the 4-nucleate embryo sac (figs. 36–38).

When the division of the megaspore mother cell nucleus occurs at the center of the cell (fig. 39) the wall formed is evanescent, the two nuclei thus being left free in the same cell cavity (fig. 40). These nuclei divide simultaneously, as shown in fig. 41; here the wall laid down at the first mitosis in the megaspore mother cell is still visible as a remnant, and several chromosomes are seen lying in the cytoplasm apart from the spindles. The four nuclei which thus arise, being the product of two successive divisions from the nucleus in which the heterotypic prophases occur, are to be regarded as megaspore nuclei (fig. 42).

Except for the absence of disorganized cells at the micropylar end, the 4-nucleate sac formed as just described is similar in appearance to that produced from a single megaspore (cf. figs. 38 and 42). Since the active growth of the sac results in the complete obliteration of the disorganized cells, it is not possible to determine by inspection of the later stages from which type of 4-nucleate sac they have been derived, but there seems to be no reason why either type or both should not continue the development, which from this point onward is exceedingly irregular. Abnormalities of many kinds were observed, and all that can be attempted here is to indicate one or two of the common tendencies shown.

In only three cases were there seen more than four nuclei in the embryo sac before fertilization. In one of these (fig. 43) the two micropylar nuclei had divided, resulting in a 6-nucleate sac like

that described above for *Phajus*, *Corallorhiza*, and *Broughtonia*. In each of the other two cases the antipodal nuclei had also divided, forming an 8-nucleate sac (fig. 44). In none of these sacs were walls observed separating the nuclei at either end.

Since no walls are present at the 4-nucleate stage, the nuclei are free to wander about through the sac (fig. 45). They were seen in all positions, but sooner or later they may all fuse to form one large nucleus. The most common course followed is that represented in figs. 46–48; the nuclei near each end of the sac fuse and the resulting fusion nuclei do the same. Often all four fuse at once; sometimes only two fuse; and in many cases degeneration sets in before any fusions have occurred.

Apparently the pollen tube may enter the sac and discharge its two male nuclei at any of these stages. In fig. 49 it has extended to an unusual distance into a sac like that shown in fig. 47, and in fig. 50 the male nuclei have been discharged into a sac containing three nuclei in the central region. As far as could be determined, no nucleus is set apart as the egg. The nuclei all lie in a group for a time, and when disorganization does not occur at once they may become fused (figs. 51–53). The large nucleus which results was not observed to carry the development any farther.

In the material sectioned embryos proved to be exceedingly scarce, and this condition is undoubtedly connected with the irregularity and lack of organization shown by the embryo sac. The two-celled proembryo in fig. 54 has evidently formed in a 6 or 8-nucleate sac, as beside the pollen tube there are in the micropylar end two disorganizing nuclei, probably synergids, and in the chalazal region a partially fused and degenerating group made up of at least three. The next few divisions in the proembryo are transverse (fig. 55), so that in its early stages it is filamentous, as in *Epidendrum*. Meanwhile the placental tissue develops rapidly from all sides, completely filling the cavity of the ovary, and the few proembryos found were lying in the small intervening crevices.

It is not unlikely that the great irregularity shown by *Bletia* as here reported may be due in part to the somewhat artificial conditions under which the plant grew in the greenhouse.

Coelogyne massangeana and Pogonia macrophylla

In each of these forms the embryo sac contains eight nuclei derived in the usual manner from a single megaspore.

As is well known, the ovules of orchids do not develop far unless pollination has occurred. In most of the species here reported the pollen tubes are found growing among the ovules before the prophases of the reduction division in the megaspore mother cell; in one or two species they are not present before the embryo sacs reach the 2 or 4-nucleate stage. In reciprocal crosses between *Phajus grandifolius* and *Bletia Shepherdii* it was found that in both cases the pollen tubes develop in great numbers and grow down into the ovarial cavity, in which ovules develop and produce embryo sacs in smaller numbers but in the same manner as after normal pollination. In no case, however, was fertilization or an embryo seen resulting from crosses between these two species. Thus the stimulus necessary to the development of ovules with embryo sacs may be furnished by foreign pollen incapable of effecting fertilization.

Discussion

The main point of interest brought out in the above descriptions is the variability in development within the species. It has been noted by several workers that while the embryo sac of one species of a genus or family is formed from the megaspore mother cell directly, the sac of another species of the same group may arise from one of a row of megaspores. The same variation within the species has occasionally been observed, as in *Salix glaucophylla* (CHAMBERLAIN **4**) and *Juglans cordiformis* (KARSTEN **5**). In the Orchidaceae the latter condition appears to hold in a number of cases, the fate of the megaspore mother cell apparently being determined very largely by the position of the spindles at the first two divisions, as pointed out above for *Epidendrum variegatum* and *Bletia Shepherdii*, and recently for *Epipactis pubescens* (BROWN and SHARP **2**).

This fluctuation results in a reduction in the number of divisions occurring between the megaspore and the egg. When a single

megaspore produces the 8-nucleate sac there are three such divisions; when a similar sac arises from a daughter cell, two megaspores thus taking part in the process, there are two divisions; and when the megaspore mother cell gives rise to the sac directly, four megaspores are involved and the egg is separated from the megaspore by but one division.

The tendency to mature the egg earlier and earlier in the ontogeny of the gametophyte is very conspicuous among gymnosperms, and it was hoped that among these very advanced angiosperms the end result of this specialization might be found—the megaspore itself functioning as an egg. The number of cases in which the elimination of but one more division would result in this situation is fairly large, and includes sacs with 4 nuclei (*Cypripedium*, PACE **7**), 8 nuclei (*Lilium*, various orchids, and many others), and 14 nuclei (*Pandanus*, CAMPBELL **3**). That the reduced condition is being approached by such a variety of ways allows us to expect with confidence to discover in some plant a situation exactly paralleling that in animals, in which the product of the reduction divisions at once becomes the egg.

Scarcely less striking than the variability within the species is the uniformity shown by the embryo sac throughout a group so varied in structure and habit as the orchids. In spite of the inconstancy in the methods of sac development the end result is remarkably uniform. The ordinary 8-nucleate sac, developed from a single megaspore, is the prevailing condition in the group. Beside the species here reported, it is found in *Calopogon* (PACE **8**), *Habenaria* (BROWN **1**), *Epipactis* (BROWN and SHARP **2**), *Gymnadenia* (WARD **10**), *Orchis* (STRASBURGER **9**), and others.

The influence of the surrounding conditions upon the behavior of the nuclei during the formation of the embryo sac has recently been considered in some detail (BROWN and SHARP **2**). The facts brought out in the present account lend further support to the idea there expressed, namely, that the causes for the behavior of the nuclei are to be sought largely in factors external to the nuclei themselves. The conditions under which the ovules of orchids develop within the ovary are undoubtedly much the same in the

various species, while the ovules themselves are almost exactly alike in structure, varying only in the matter of dimension. Thus since the archesporial cell in the different species has the same general form and initiates a series of stages developing under practically the same conditions, a general similarity in result is to be expected.

Whether a row of megaspores is produced or not seems, as already pointed out, to be largely dependent upon the position of the spindles at the first two divisions. But megaspore mother cell and functioning megaspore just before division are very much alike in size, shape, and surroundings, and are acted upon by similar external factors, so that whichever gives rise to the embryo sac the same course is followed and the same end is reached.

The 6-nucleate embryo sacs of *Phajus*, *Corallorhiza*, and *Broughtonia* seems to show a tendency toward a further reduction of the vegetative portion of the gametophyte.

In all of the species examined the endosperm nucleus, whether arising from the fusion of two or more nuclei, disorganizes without dividing, so that *Calopogon pulchellus* (PACE **8**), in which it may give rise to as many as four free nuclei, remains as the only known case where endosperm is developed in orchids.

Summary and conclusions

1. The archesporial cell in all of the species examined is hypodermal and cuts off no parietals, thus becoming at once the megaspore mother cell.

2. The megaspore mother cell in all of the forms studied divides to two daughter cells, the chalazal one of which divides to form two megaspores. The innermost megaspore gives rise to the embryo sac.

3. In *Epidendrum variegatum* and *Bletia Shepherdii* the megaspore mother cell often gives rise directly to the embryo sac; in such cases four megaspores take part in the formation of the sac.

4. In *Epidendrum variegatum*, *E. cochleatum*, *E. verrucosum*, *E. globosum*, *Coelogyne massangeana*, and *Pogonia macrophylla* the embryo sac is of the ordinary 8-nucleate type. In *Bletia Shep-*

herdii the development is very irregular, but in fully mature sacs eight nuclei are present.

5. In *Phajus grandifolius*, *Corallorhiza maculata*, and *Broughtonia sanguinea* the primary antipodal nucleus divides only once, so that the embryo sac contains but six nuclei: four micropylar and two chalazal.

6. Polar fusion occurs in all of the forms studied. In the 8-nucleate sacs the fusion is between two equivalent polar nuclei. In the 6-nucleate sacs the micropylar polar migrates to the chalazal end and there fuses with the two nuclei which have resulted from the division of the primary antipodal nucleus.

7. In all of the species in which fertilization was observed it is of the usual type; one of the two male nuclei fuses with the egg nucleus, while the other fuses with the two polars.

8. The proembryo commonly consists of three cells before the first longitudinal division occurs; in *Epidendrum* a filament of as many as 20 cells may be formed. In the mature seed the body regions have not yet been marked out in the proembryo.

9. In all of the species examined the endosperm nucleus disorganizes without dividing.

10. The ordinary 8-nucleate embryo sac produced by a single megaspore is the prevailing condition among orchids. The causes for the comparative uniformity throughout the group are to be sought largely in the conditions surrounding the developing nuclei.

11. The orchids show very commonly a marked variation within the species. This variability, seen chiefly in connection with megaspore formation, is resulting in making an embryo sac in which the egg is removed from the megaspore by a single division a conspicuous feature in the group.

12. Although endosperm has been eliminated and the seed reduced to a very simple structure, the orchids as a group show in their female gametophytes very little advance over other plants, especially those lower in the line of the monocotyledons.

13. Reciprocal crosses between *Phajus grandifolius* and *Bletia Shepherdii* show that in these species the stimulus necessary to the development of ovules with embryo sacs may be furnished by foreign pollen incapable of effecting fertilization.

To Professor DUNCAN S. JOHNSON are due acknowledgments for many valuable suggestions during the progress of the work. The writer is also indebted to Mr. WILLIAM HARRIS for placing at his disposal material in the Hope and Castleton Botanic Gardens.

THE UNIVERSITY OF CHICAGO

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EXPLANATION OF PLATES XXI–XXIII

All figures were drawn with the aid of an Abbé camera lucida, and show magnifications as follows: figs. 1–15, ×1200; figs. 16–18, ×295; figs. 19–24, ×1125; figs. 25, 26; ×513; fig. 27, ×295; figs. 28–33, ×1200; figs. 34–54, ×845; fig. 55, ×475.

PLATE XXI

Epidendrum variegatum Hook.

FIG. 1.—Synapsis in megaspore mother cell.

FIG. 2.—Inner daughter cell dividing; outer daughter cell disorganizing.

FIG. 3.—Functioning megaspore: outer daughter cell and megaspore disorganized.

FIG. 4.—Two-nucleate embryo sac: no wall on lingering spindle fibers.

FIG. 5.—Four-nucleate embryo sac.

FIG. 6.—Division to form eight nuclei.

FIG. 7.—Megaspore mother cell dividing equally; distinct wall formed.

FIG. 8.—Wall has disappeared; vacuole has formed.

FIG. 9.—Unusual arrangement of nuclei and vacuoles; nuclei in this case have gone into resting condition.

FIG. 10.—Division to form four nuclei; distinct cell plates formed.

FIG. 11.—Four-nucleate embryo sac (four megaspore nuclei): walls have disappeared.

FIG. 12.—Eight-nucleate embryo sac.

FIG. 13.—Double fertilization.

Fig. 14.—Young proembryo: endosperm nucleus and antipodals disorganized.

FIG. 15.—Proembryo.

Epidendrum verrucosum Sw.

FIG. 16.—Filamentous proembryo.

Epidendrum cochleatum L.

FIGS. 17, 18.—Two stages of the proembryo.

PLATE XXII

Phajus grandifolius Lour.

FIG. 19.—Synapsis in megaspore mother cell.

FIG. 20.—Functioning megaspore: other daughter cell and megaspore disorganized.

FIG. 21.—Micropylar nuclei dividing; chalazal nuclei remaining undivided.

FIG. 22.—Six-nucleate embryo sac.

FIG. 23.—Same: egg apparatus formed; chalazal nuclei and micropylar polar fusing.

FIG. 24.—Fertilization: second male nucleus associating with other free nuclei of the sac.

FIGS. 25, 26.—Proembryo showing micropylar cell growing out as a haustorium.

FIG. 27.—Proembryo from mature seed.

Corallorhiza maculata Raf.

FIG. 28.—Inner daughter cell of megaspore mother cell dividing; outer daughter cell disorganizing.

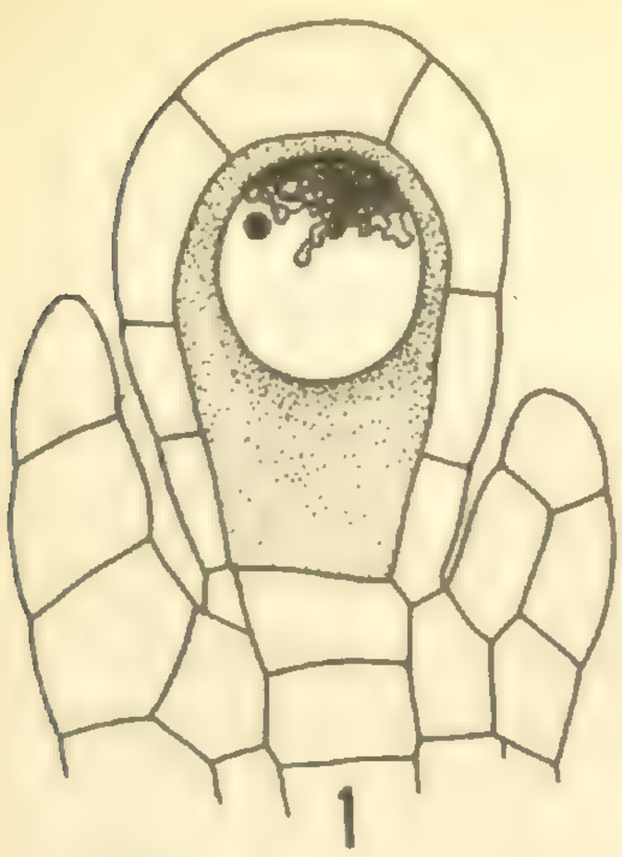
FIG. 29.—Four-nucleate embryo sac.

FIG. 30.—Micropylar nuclei dividing.

FIG. 31.—Six-nucleate embryo sac: micropylar polar has migrated to base of sac.

FIG. 32.—Fertilization has occurred; second male nucleus lying near egg.

FIG. 33.—Young proembryo: second male and other free nuclei of the sac fusing.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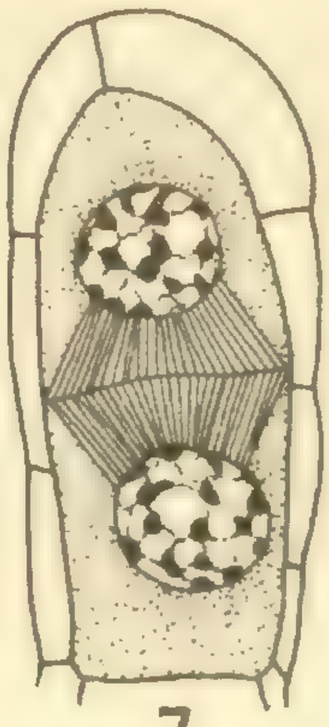
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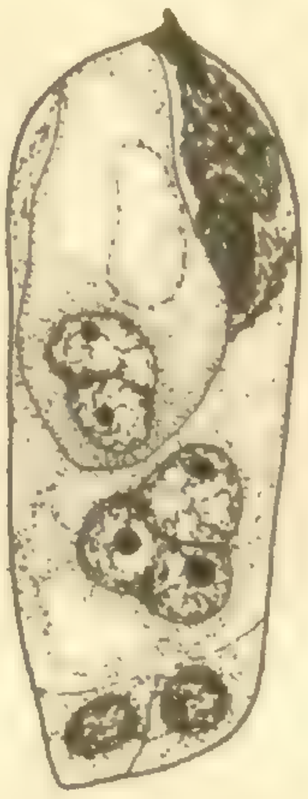
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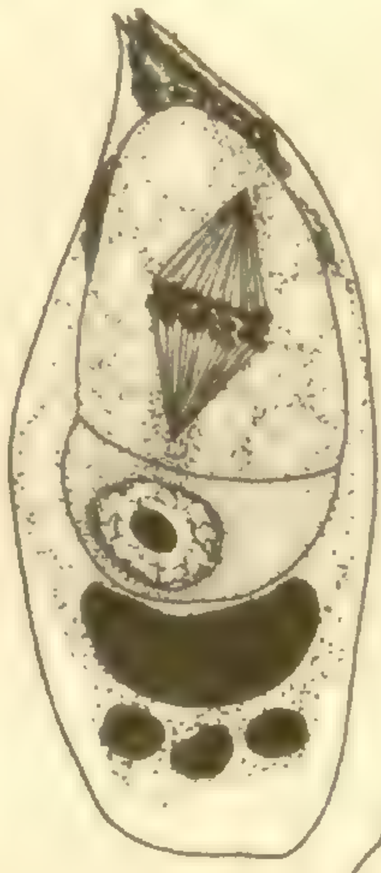
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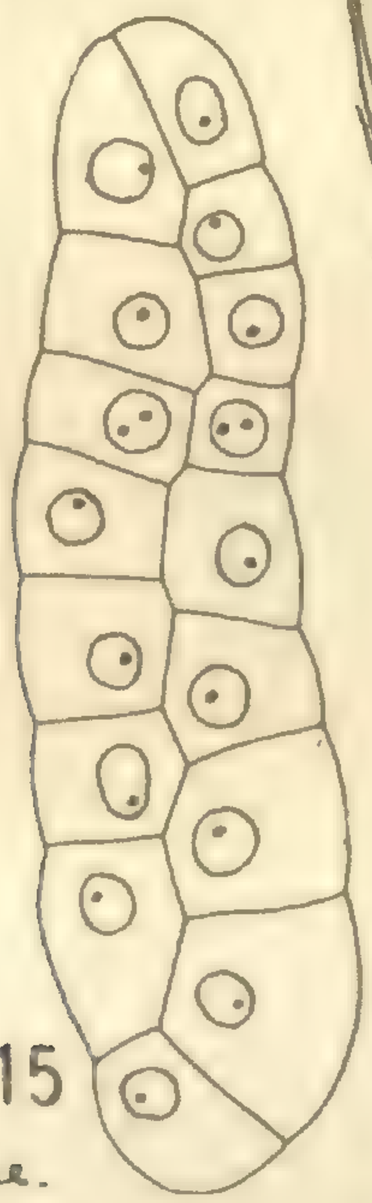
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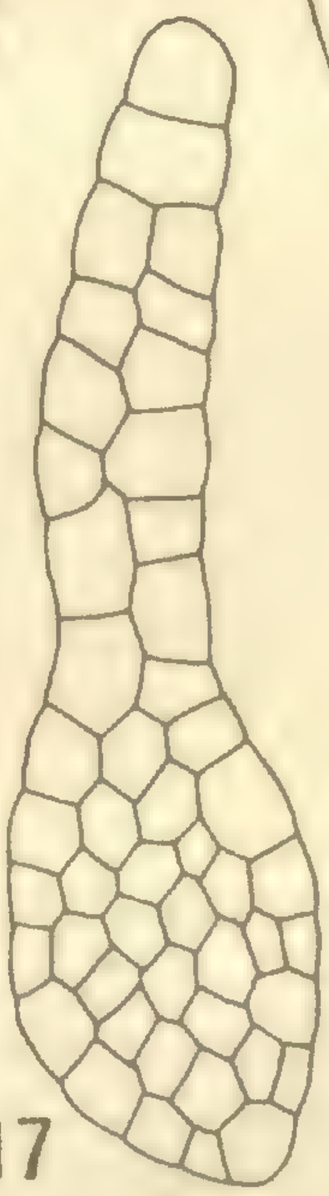
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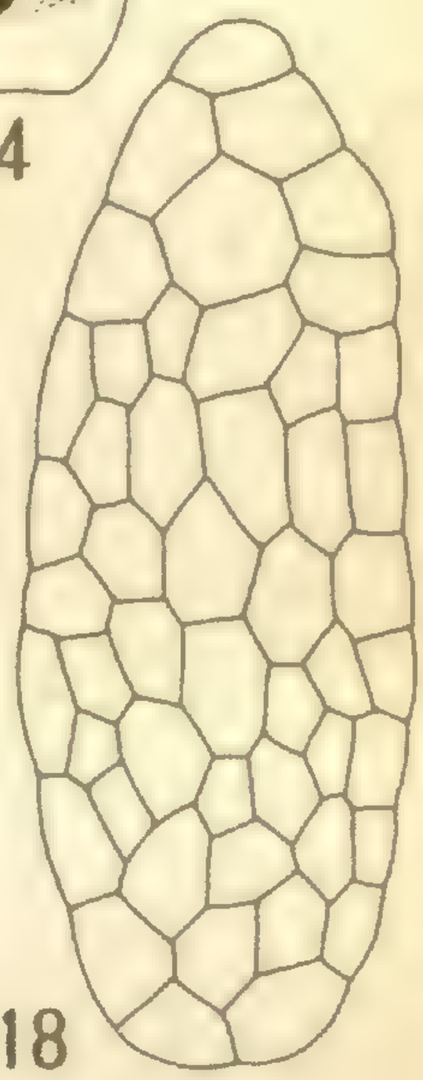
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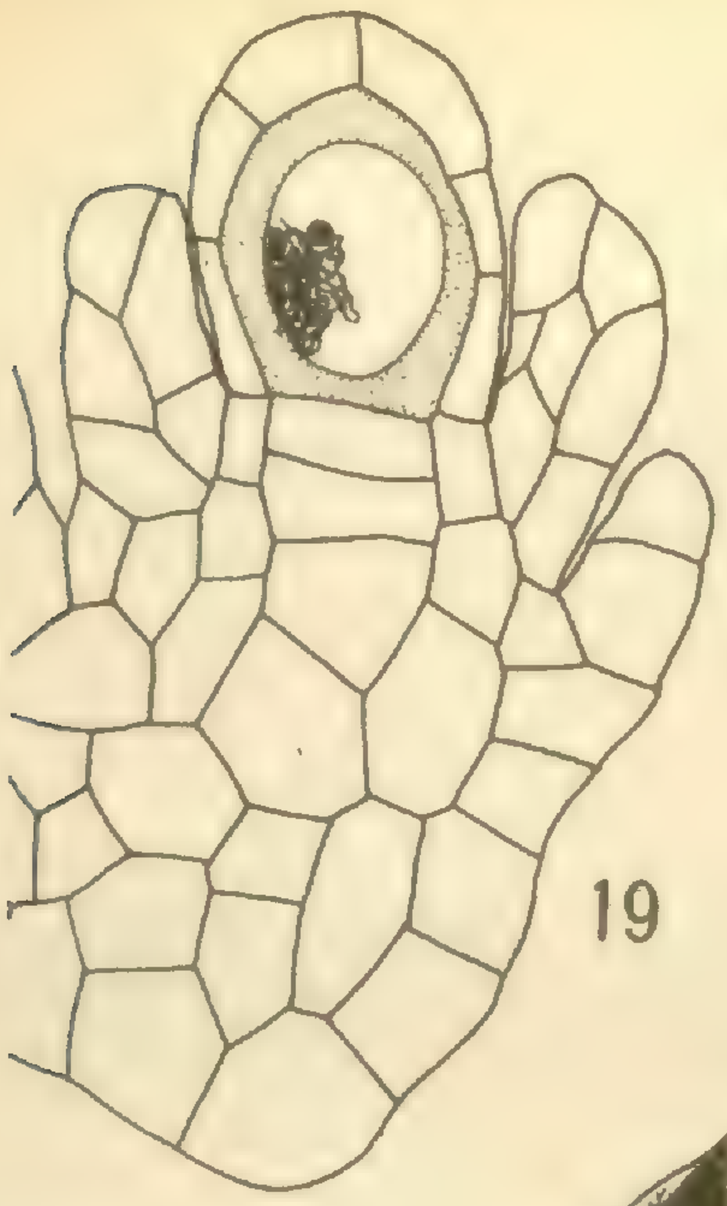
Sr. W. Sharp del.

SHARP on ORCHID EMBRYO SAC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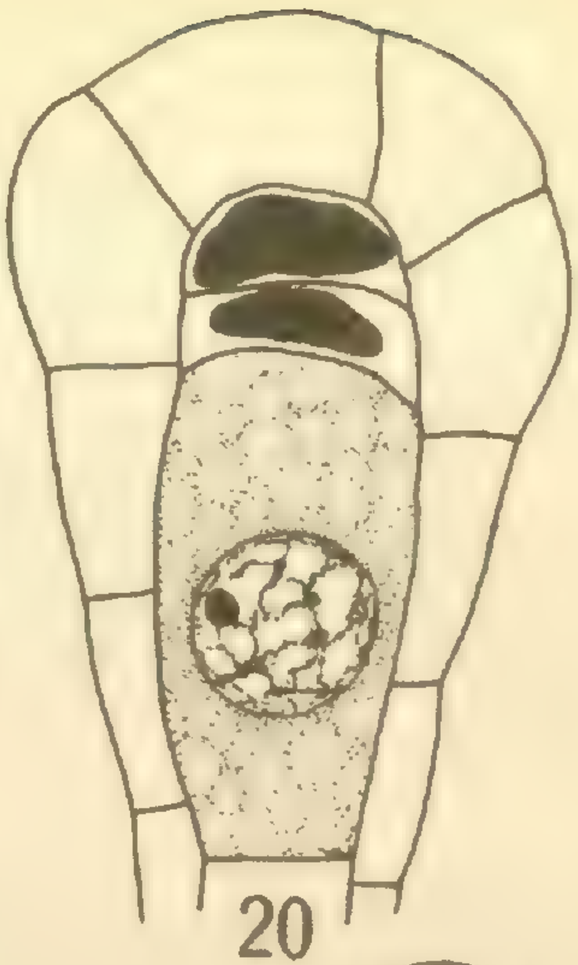
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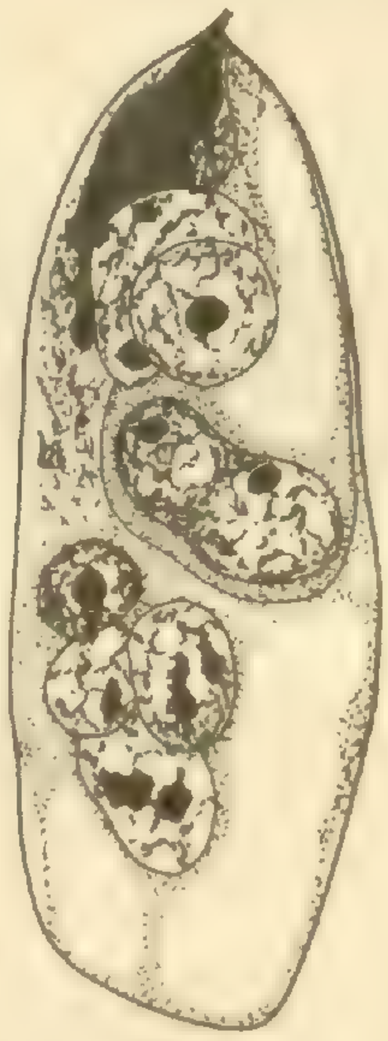
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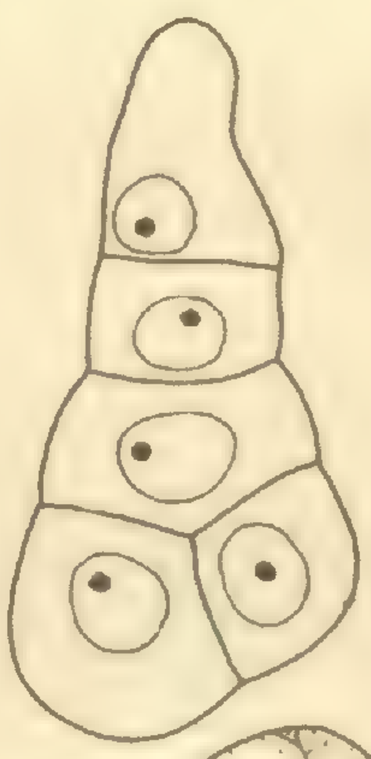
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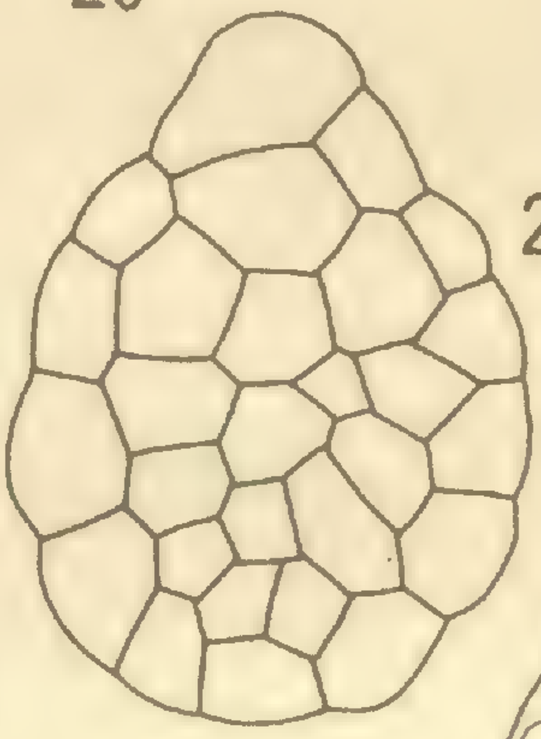
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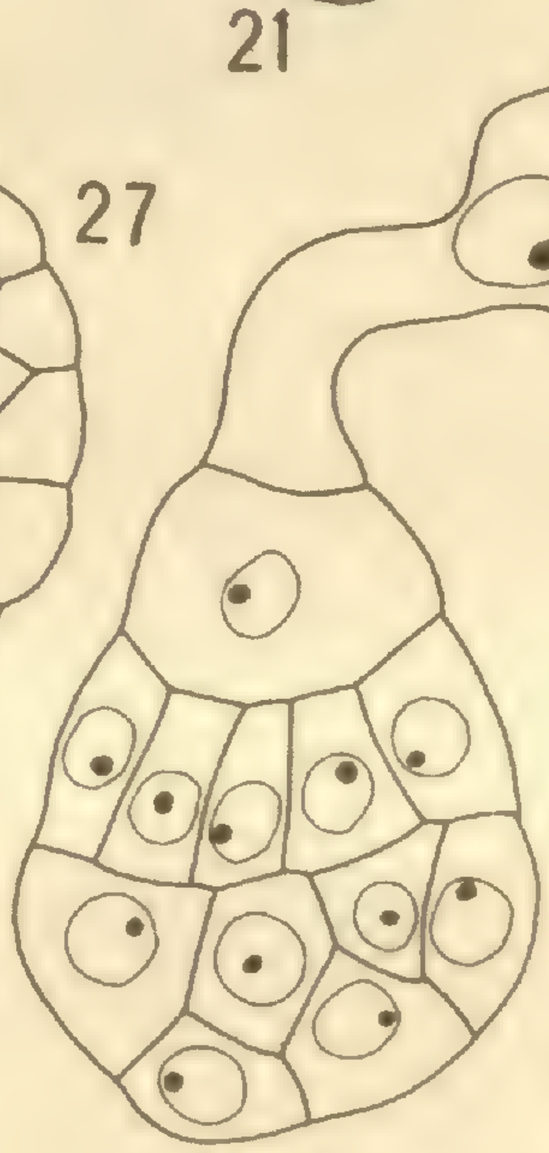
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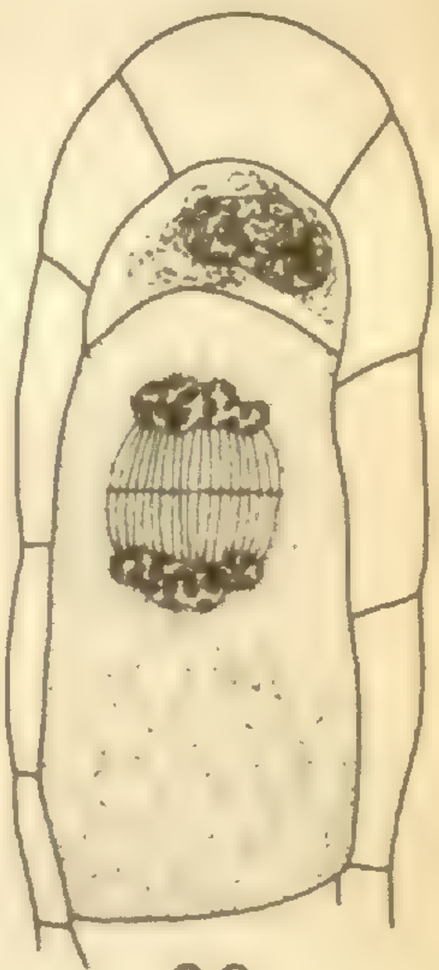
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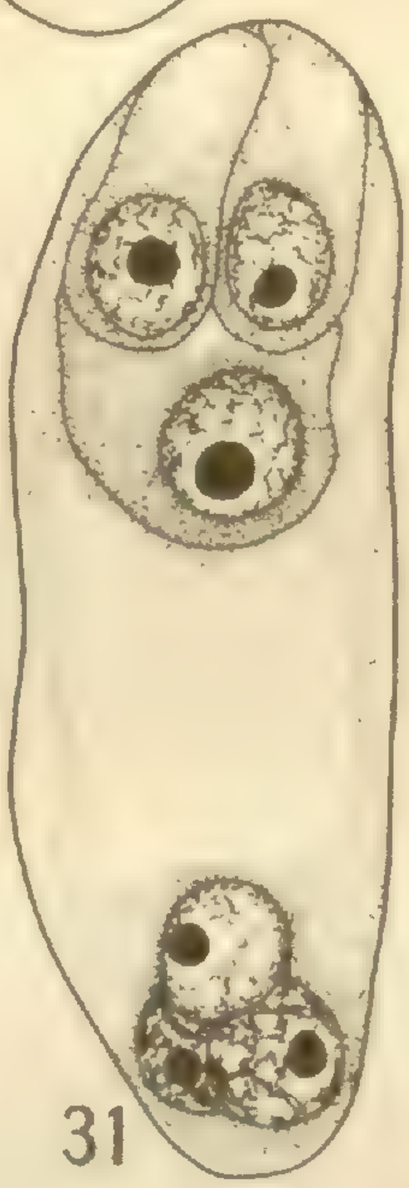
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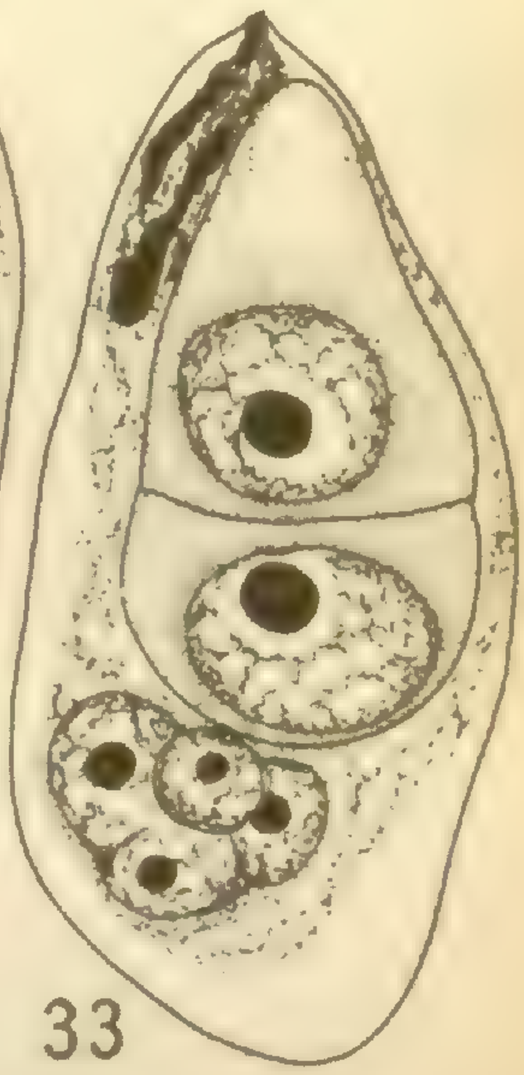
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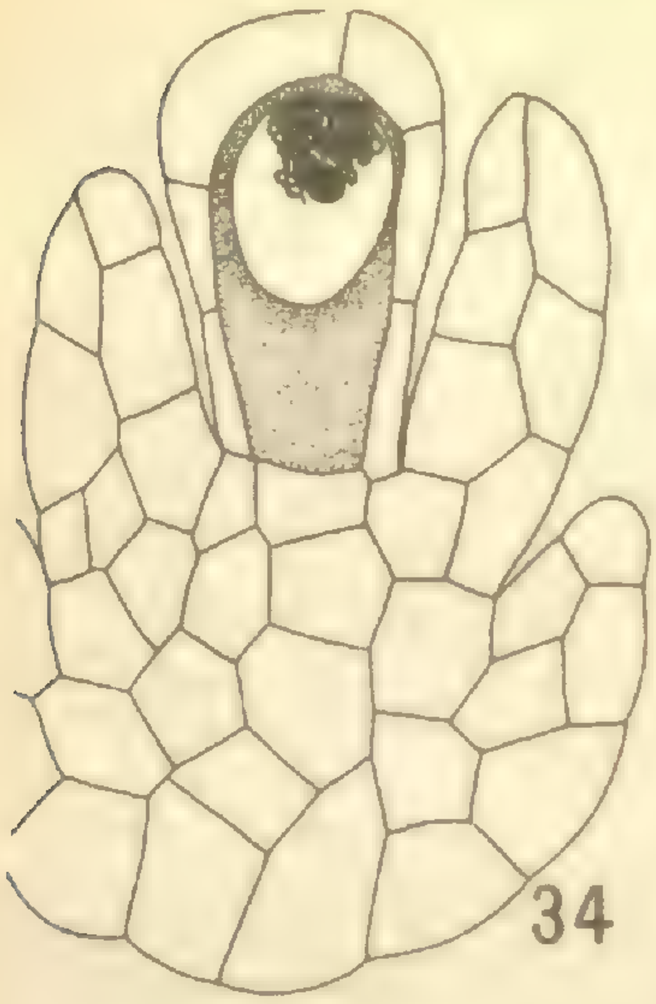
SHARP on ORCHID EMBRYO SAC



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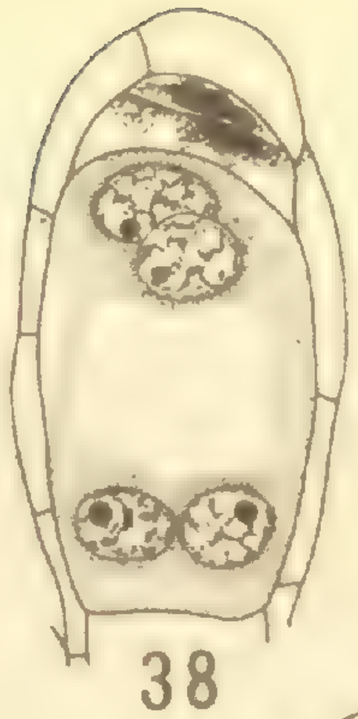

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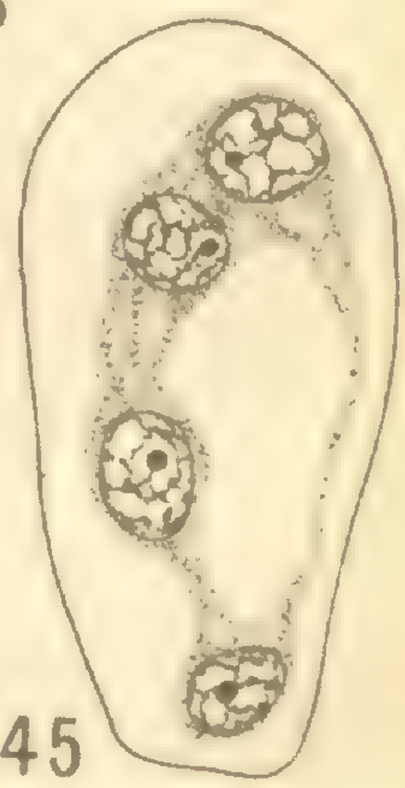

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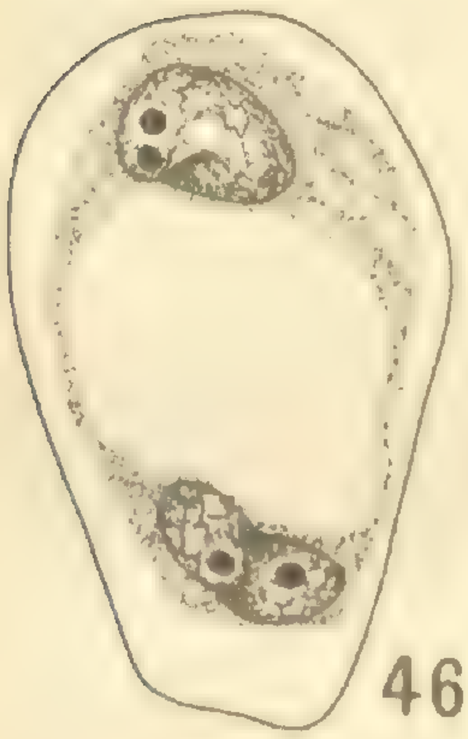

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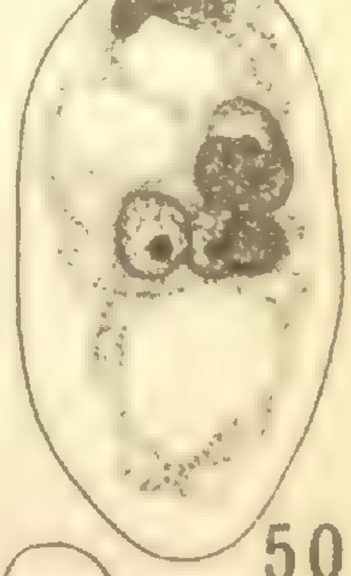

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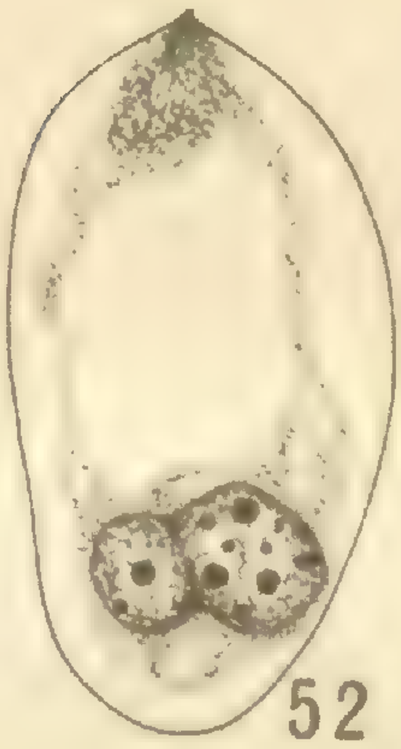

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S. W. Sharp del.

SHARP on ORCHID EMBRYO SAC

PLATE XXIII

Bletia Shepherdii Hook.

FIG. 34.—Synapsis in megaspore mother cell.

FIG. 35.—Inner daughter cell dividing to form two megaspores.

FIG. 36.—Functioning megaspore: outer daughter cell and megaspore disorganized.

FIG. 37.—Two-nucleate embryo sac.

FIG. 38.—Four-nucleate embryo sac.

FIG. 39.—Megaspore mother cell dividing equally; wall forming.

FIG. 40.—Wall has disappeared.

FIG. 41.—Two nuclei dividing: wall formed at first mitosis still visible as a remnant in this case.

FIG. 42.—Four-nucleate embryo sac (four megaspore nuclei).

FIG. 43.—Six-nucleate embryo sac: micropylar nuclei have divided.

FIG. 44.—Eight-nucleate embryo sac: no separating walls.

FIG. 45–48.—Usual fate of the 4-nucleate embryo sac; all the nuclei fuse.

FIGS. 49–53.—Abnormal sacs into which male nuclei have been discharged; all the nuclei tend to fuse; *pt*, pollen tube; ♂, male nuclei.

FIG. 54.—Young proembryo evidently having formed in a normal sac.

FIG. 55.—Later stage of proembryo.

GROWTH STUDIES IN FOREST TREES

I. PINUS RIGIDA MILL[1]

HARRY P. BROWN

(WITH PLATES XXIV AND XXV)

The phenomenon of tree growth has long been a subject of investigation. SACHS, HUGO DE VRIES, NÖRDLINGER, MER, the HARTIGS, WIELER, BÜSGEN, VON MOHL, and a host of others have worked on problems concerned with it, and many papers presenting the results of investigations are to be found in the literature of the last half-century.

As might be expected, the question has resolved itself into a number of minor topics, each with its coterie of followers. Some have placed particular stress on spring and summer wood formation; others have studied growth as related to external factors or to inheritance. Various instruments have been devised to measure tree growth, and one author (REUSS **12**) goes so far as to assert that thunderstorms cause a growth stimulus in trees. Investigations dealing with every phase of the subject are described in exhaustive detail, and yet with rare exception there is a maze of conflicting opinion sufficient to confuse even the careful reader.

The present studies were undertaken with a twofold purpose, namely, to clear up disputed points regarding annual ring formation in trees and to formulate laws of tree growth. Investigations were carried on upon various forest trees with this idea in view. The results of those on *Pinus rigida* are embodied in this paper.

Secondary thickening in trees arises as a general rule from a cambium which lives from year to year. This annually passes through certain active and certain dormant periods. The latter assertion, however, is to be taken in its broadest sense. In many tropical woods the interruption to growth can be detected only with a microscope, while in others it is totally lacking; the wood appears

[1] Contribution from the Department of Botany, Cornell University. No. 148.

as a homogeneous mass. The formation of this cambial layer takes place the first year, and is brought about by the linking together, so to speak, of the fascicular cambium of the primary bundles by the formation of interfascicular cambial zones, the result being a cylinder of merismatic tissue capable of division. There are, in addition to this, however, certain other growth phenomena. In the cortex of many trees, either near or remotely distant from the primary cambium, secondary cambial zones arise, whose function it is to form cork, the so-called cork cambiums. They are not united in a ring, as is the primary cambium, but extend for comparatively short distances in a peripheral direction.[2] Again, as met with in the Cycadales and Gnetales (COULTER and CHAMBERLAIN 4), successive bundle-forming cambiums sometimes arise toward the periphery of the stem, and in such cases the life of the primary cambium is generally very short. Further, among dicotyledons there are a number of modifications of secondary thickening, particularly in underground parts. In the present studies, however, it is the intention to confine investigation to growth as it normally occurs in trees, that is, to the activities of a cambium which has certain active and certain dormant periods.

A number of specimens of *Pinus rigida* in the Cornell pinery as well as others in the wild state were used. Those in the nursery consisted of a number of individuals standing in a row which ran approximately east and west. The land sloped gently to the southwest and drainage conditions appeared to be good. The individual trees were about 22 years of age and seemed to be in a thriving condition. The height varied from 6 to 7 m., depending on the vigor of the individual, and the average diameter at breast height was 12 cm. In 1909, when investigation began, the branches extended to within 1.2 m. of the ground. However, during the year above mentioned, the trees were pruned to a height of 1.9 m. above the ground. Experiments were carried on with six individuals of this series, which were numbered I–VI.

The trees in the wild state had better be described separately, since each was of different age and external factors varied with the individual. For the sake of clearness they were designated as

[2] Exceptions to this rule occur, resulting in the so-called "ring-barked" trees.

A, *B*, and *C*. These specimens were growing in a strip of woodland about one mile north of the university campus. Conditions of soil and light appeared to be good in every case, that is, to all appearances the trees were not retarded.

Tree *A* was a magnificent specimen about 25 m. high; in other words, it had practically reached its maximum size. The trunk was slightly shaded to a height of 4.5 m. by an undergrowth composed of white pine. There were no branches above for 18 m. until the crown began. The latter was but fairly developed, being about what one might expect under forest conditions. At breast height, the caliper measure was 50 cm. A conservative estimate of the age would be 100 years.

Tree *B* was a younger individual. Its height was approximately 20 m., and crown development had progressed but poorly. At breast height the caliper measure was 26 cm. The base was entirely free of undergrowth, and light conditions were better inasmuch as there were no close neighbors. Tree *B* then differed from tree *A* in (*a*) age, (*b*) light conditions, (*c*) crown development, (*d*) height, and (*e*) diameter.

Tree *C* was about the age of those in the nursery, namely 20–25 years, and rose to a height of 7 m. Branches were borne practically to the ground. The caliper measure was 11 cm. Illumination was better on the south side, due to the close proximity of a road, while on the north the underbrush encroached slightly.

Methods

Investigations began in the spring of 1909, and the last cutting that year was made on July 6. Alternate cuttings were taken from two different individuals at intervals about a week apart, so that two weeks elapsed between incisions on any one tree. These were made in the following manner. Beginning from the base of the apical shoot, portions of the cortex and wood to a depth of at least one annual ring were removed at intervals of about 50 cm. Twelve cuttings were made in this manner with the aid of a sharp pocket-knife, care being taken not to rupture the cambium. Each cutting was placed in a separate vial, properly labeled with the date, num-

ber of cutting, and tree, and kept separate from the others in all the successive processes of fixing and imbedding.

The following year (1910) cuttings were again resumed on the same trees, as well as on four more in the same row. The manner of procedure was identical with that above described except (*a*) every other cutting was omitted and (*b*) this season the first cutting was made February 21, the second April 2, and thereafter until the third of May. The object was to check up the results of the previous season and to make new observations. Two cuttings were also made on trees *A*, *B*, and *C* on April 27, one on the north side and one on the south. For purposes of comparison, one root cutting was taken from tree III on the same date.

Microscopical characters of the wood

As is characteristic of the Coniferae, the secondary wood of *Pinus rigida* is entirely devoid of vessels. It consists almost entirely of tracheids with bordered pits on their radial walls. In cross-section these appear regularly arranged in radial rows, which occasionally divide as they proceed toward the cambium. In longitudinal section they present the normal tracheid form, that is, a rectangular prism with sloping ends. The annual rings are sharply differentiated. Proceeding from the pith outward in radial direction are numerous pith rays; secondary rays arise in response to necessity; both are of the usual coniferous type. The histological characters of coniferous wood, however, have been described in detail by PENHALLOW (11), and the reader is referred to his excellent work for further detail.

The structure of the secondary thickening in the roots is quite closely related to that of the stem. However, there are one or two differences. The demarcation between the different rings is not so sharp. This results because the wood of the root is less dense than that of the stem. The tracheids possess wider lumina and there is less summer wood produced. In radial section the bordered pits on the walls are often biseriate, a condition which is never met with in the wood of the aerial portion.

Microscopical characters of cambium and cortex in winter condition

CROSS-SECTION

The radial rows of tracheids in the xylem continue directly out into the cortex (fig. 9) through the cambial zone. For a time this radial arrangement is maintained, but sooner or later it becomes irregular, due to certain changes which take place. The cambial zone in cross-section appears as a number of layers of cells with comparatively thin walls. It is impossible to pick out the initial layer. Exterior to this are the sieve tubes. These have wider lumina than the cells of the cambial zone, and the walls are thickened as much as or more than those in the summer wood section of the xylem. However, they are not lignified as are the latter. Companion cells are wholly lacking. The rows of bast parenchyma are very prominent. One row with a few scattered individuals is formed each year (STRASBURGER **13**), so that the thickened layers of sieve tubes are separated by thin bands of bast parenchyma. In the outer cortex the bast parenchyma cells become gorged with starch and greatly enlarged. As a result the older sieve areas are stretched tangentially and are seen as thin bands separating the larger cells. Pith rays appear as straight lines running out into the cortex, but as they proceed radially into the cortex they soon become more or less irregular and curved. There are no crystallogenous cells such as are described by STRASBURGER in *Pinus silvestris*. Exterior to the cortex proper there is a series of corky layers which have arisen from living cells in the outer cortex, the so-called cork cambiums. Their structure is of the general type described by STRASBURGER (**13**).

RADIAL SECTION

In radial section the cambial cells appear as prisms with sloping ends. The size varies slightly with the age. The sieve tubes have the general shape of the cambium cells from which they originate. Their radial walls are equipped with sieve plates, and these have the same location as the bordered pits on the walls of the tracheids. In radial section likewise we see to best advantage the bast parenchyma. This consists of rows of barrel-shaped cells arranged one

above the other. There is also a change in the pith rays. The ray tracheids have given rise to ray cells, so that the pith rays consist exclusively of the latter. These as well as the bast parenchyma cells contain abundant starch.

TANGENTIAL SECTION

In order to study cambium and cortex in tangential section, a series of mounts is necessary. The same general characters are observable, but in addition it is evident that there is an entire absence of sieve plates on the tangential walls of the sieve tubes. The callus thickenings of those on the radial walls, however, are particularly noticeable with proper staining (methyl blue).

Cambial awakening

In taking up the study of xylem formation as it normally occurs in trees, one naturally begins the study before cambial activity begins. Cuttings taken at different heights from tree III on February 21, 1910, all showed in cross-section the general outline of the completed ring. Growth was not manifest in any of the sections. Each ring presented well marked areas of early and late wood. The latter in *Pinus rigida* is sharply differentiated, owing to its greatly thickened walls. The above statement does not hold true, however, for the wood of the first two or three years at any point in the trunk. Here there is no sharp demarcation between early and late wood. This condition is probably brought about by the fact that the main axis was elongating rapidly at this point when the ring was formed, or else, as these investigations tend to show, growth is slow in beginning in the apical shoot but progresses very fast when once started, so rapidly in fact that there is not sufficient time for the walls to thicken appreciably. In either alternative, there is a gradual thickening in the walls of the late wood of successive rings as the apical shoot progresses aloft.

The next set of cuttings were taken on April 4, 1910, from tree III. The cambium was still in the resting condition. Figs. 1–3 and 7–9 show the changes which occurred (figs. 1–3) between April 4 and April 15. In fig. 3 growth is more advanced than in either figs. 1 or 2. The latter are both in the resting condition. So far

as can be detected there is no evidence of tracheal formation. Figs. 7–9 are from cuttings made on the same individual at this time, but each successively nearer the ground. In the first two growth is in evidence, while in the last the cambium is still in the resting condition. It is evident from the photographs that in the spring of 1910 growth made itself manifest in tree III as early as April 15. Cuttings taken from trees IV and V at the same date likewise showed evidence of cambial activity. While there was no satisfactory evidence obtained the previous year as regards cambial awakening, since observations were begun too late, sections from tree II on May 13, 1910, showed growth in such an advanced state that cambial activity must have begun fully as early the previous year.

As regards cambial awakening in trees *A*, *B*, and *C*, no lengthy observations were carried on; but two cuttings per tree were made on April 27, one on the north side and one on the south. At this date trees *B* and *C* already showed evidences of growth at breast height in both cuttings. In tree *A* the cambium was still in the resting condition. However, tree *A* was older and taller than the other individuals, and it is very evident that growth must have already begun in the higher parts.

The observations described above are in accord with those of other investigators. BÜSGEN (**3**) gives the time in general for cambial awakening for middle Germany as between the last half of April and the first half of May. R. HARTIG (**7**) has observed that evidences of growth are manifest in young (10 years) specimens of *Pinus silvestris* as early as April 20, while its appearance at the base of the older trees depended very much on external factors, such as thickness of stand, soil conditions, ground cover, etc. BUCKHOUT (**2**), by means of bark measure, gives the date of growth inception in larch and white pine as the last week in April. However, as his computations were made at the base of the trees, probably growth began aloft earlier. That growth was not evidenced at the base of tree *A* was due, according to the researches of R. HARTIG (**7**), to at least three causes, namely (*a*) long trunk, (*b*) age, and (*c*) shaded base. While the present investigations do not afford conclusive evidence, inasmuch as they covered but a

period of two years, it would appear that in the vicinity of Ithaca growth began in *Pinus rigida* at about the same time each spring. To determine this point definitely, however, observations must needs be carried on for a period of years. That growth made itself evident in 1910, however, as early as April 15 is readily apparent from the photographs.

Place of cambial awakening

The question of origin of growth is still in dispute. T. HARTIG (**8**) claimed that it made itself manifest in the youngest branches first and extended slowly downward. NÖRDLINGER (*Forest Botany*, 1874) makes the same assertion. R. HARTIG (**7**) appears to accept his father's statement if we are to judge from the following quotation: "Am oberirdischen Stamme beginnt der Zuwachs zuerst in den jüngsten Trieben," etc. These three investigators, therefore, were unanimous in the opinion that the awakening of growth is earlier at the top of a tree than below.

MER (**10**) disputes this general assertion. According to his researches, the procedure of awakening was sensibly different in older trees. While in 25-year-old oaks, beeches, and firs, growth was first manifest in the youngest branches, in the older trees it was in evidence at the same time at the bases of the branches and even in the trunk where the roots began. From these points growth gradually extended to the intermediate regions.

Figs. 4–6 correspond respectively to those of the preceding numbers, except that a period of 19 days intervened. Comparing those of different date, we see that growth is more in evidence in every case where the cutting was taken at the later date. In figs. 1 and 2 we have apparently the resting condition, while figs. 4 and 5 exhibit signs of growth, the latter being more in evidence in fig. 5. Comparing figs. 3 and 6, it follows that there is a considerable advance in growth. In the former, at the outside, only two half-formed tracheids are to be seen, while in the latter three or four rows are present and these are of larger size. Comparing figs. 1–6 as a whole, it is evident that during a period of 19 days there was an awakening of cambial activity in the apical portion, first manifest in fig. 3 on April 15. Growth first appeared in the crown of tree III

some distance below the apical shoot, but in a period covering 19 days gradually spread upward and was in progress in the apical shoot on May 4, 1910.

Cuttings of May 4 corresponding to figs. 7–9 were not photographed. Examination revealed the fact, however, that growth was in progress throughout the basal portion of the trunk on that date, and had progressed to a greater extent than was evidenced on April 15.

From the above investigations it follows that growth was in progress throughout the main axis of the tree on May 4, while 19 days previous it was not in evidence in either the apical portion or the base. If R. HARTIG is right in his assertion that growth is first manifest in the branches, *Pinus rigida* is surely an exception to the rule. MER'S investigations on *young* trees are in accord with HARTIG'S, so here likewise growth in *Pinus rigida* appears to present an anomaly. That HARTIG is right in his assertion that cambial activity proceeds from the base of the crown downward, investigations on trees *A*, *B*, and *C* seem to give convincing evidence. Cambial activity was already in progress on both sides of the base in trees *B* and *C* on April 27, while both cuttings in tree *A* on that date appeared to be in the resting condition. This is explained in that the trunk of tree *B* was better illuminated below than that of tree *A*, while tree *C* was but 25 years old. But at this date growth must have been in evidence in the upper portions of tree *A*, and the only reasonable hypothesis is that it had not yet reached the base, owing to poor insolation, thick bark, and age of the tree.

Growth in lateral branches

With a view of adding something further of value to the manner of growth procedure in *Pinus rigida*, investigations were also carried on upon certain of the lateral branches. Cuttings were taken from each year's growth until the main axis was reached. Then incisions were made 20 cm. above and a like distance below the point where the branch joined the main axis. Growth in the branches followed the same rule as in the main axis. It commences some distance back of the apical shoot and spreads gradually in both directions. Time of awakening in the apical shoots of the

branches, at least in the case of trees standing in the open, appears to be identical with that in the apical shoot of the main axis. Cuttings taken May 4 showed about the same amount of growth in each case.

The time of the beginning of cambial activity at the base of the branches is of interest when compared with that of the main trunk. Fig. 11 shows a section from the base of a limb six years old. Fig. 10 is from a cutting taken from the main axis just above the branch, and fig. 12 a like distance below. Growth is most advanced in fig. 12, present in fig. 10, but lacking to all appearances in fig. 11. Cuttings taken from the limb in question showed growth in evidence to the extent of one or two tracheids (out to and including the apical shoot). It follows from the above that growth at the base of the branches is more retarded than at neighboring spots in the main axis. It proceeds more rapidly in the latter than it does in the former, so that it is often in evidence in the main axis before it makes its appearance at the base of the branches. This may be due to the more rapid rise of solutions in the trunk, although further investigation is necessary to decide that point.

Rate of procedure

Having determined the general procedure of growth in *Pinus rigida*, observations were next made on the rate of procedure. In order to make estimates of this, the series of cuttings of 1909 on tree II were employed. There were four sets of these of twelve each. In each set the amount of wood formed for the individual section was determined as nearly as possible with a micrometer scale, and the results tabulated on a basis of 100 (table I). The number of days intervening between each observation are given as well as the total gain and average gain per day; *x* implies cutting was a failure; + signifies width at least as much as given; ? indicates apparent loss due to local growth fluctuation.

The table is of value in leading us to certain general conclusions. On May 13, the width of the new-formed ring was greatest in cuttings 4–6. It gradually dwindled in size toward the apical shoot, while below there appeared to be a decline followed by an increase. The next investigation was made on May 25, twelve days later.

TABLE I

No.	Amount	Amount	No. of days	Gain	Gain per day	Amount	No. of days	Gain	Gain per day	Amount	No. of days	Gain	Gain per day
	May 13, '09	May 29, '09				June 3, '09				June 15, '09			
1	3	5	12	2	0.17	5	9	0	0.00	35	12	30	2.50
2	3	5	12	2	0.17	20	9	15	1.63	25+	12	5	0.42
3	8	8	12	0	0.00	24	9	16	1.78	x	12	x	x
4	12	15	12	3	0.25	40	9	25	2.78	35	12	?	?
5	12	18	12	6	0.50	30	9	12	1.33	40	12	10	0.83
6	12	20	12	8	0.67	30	9	10	1.11	35	12	5	0.42
7	8	13	12	5	0.42	40	9	27	3	40	12	0	0.00
8	x	10	12	x	x	30	9	20	2.22	38	12	8	0.67
9	8	11	12	3	0.25	40	9	29	3.22	45	12	5	0.42
10	6	10	12	4	0.34	21	9	11	1.22	30	12	9	0.75
11	x	x	12	x	x	25	9	x	x	42	12	17	1.42
12	11	8	12	?	x	x	9	x	x	17	12	x	x

Looking at the average gain per day, we see that in cutting 6 the greatest increase occurred, while above and below the amount of gain varied irregularly with the different cuttings. However, the gain in the apical shoot was but slight. Comparing the results of May 25 with those of June 3, it is evident that, with the exception of the apical shoot, the average daily increase at the latter date was greater in every case than in the former. In other words, the tree grew faster in diameter, with the exception of the terminal shoot, during the last of May and the first of June than before that time. It follows from the table that the rate of increase varies considerably with the cutting and obeys no general law. The data of June 15, however, are most interesting. There was a decrease in the rate of growth between June 3 and June 15, with the exception of the apical shoot. Here, on the contrary, the gain in 12 days was 15 times as great as that of all the diameter growth previous to June 3. There was then a very marked increase in the formation of the annual ring at this point as compared with the gradual decrease in the remainder of the tree. Unfortunately, however, data are not available bearing on the rate of elongation of the apical shoot. It would appear, however, that its elongation must have been very rapid up to June 3, so much so in fact that the increase in the width of the annual ring could not result. From June 3 to June 15 the rate of elongation probably decreased appre-

ciably, while greater increase of wood formation resulted as a natural sequence.

Before summing up the results of the preceding paragraph, some observation on cessation of cambial activity should be given. It has long been recognized that while cambial activity makes itself manifest in many trees at about the same time, there is no relation evident in its cessation. Thus BUCKHOUT (**2**) found in *Larix decidua* that there was little if any growth after July, while *Pinus Strobus* continued to form wood until well into September. R. HARTIG (**6, 7**) also gives data bearing on this subject. In beech it lasts 2.5 months, in oak 4 months, in Scotch pine and Norway spruce 3 months. FRIEDRICH (see WIELER **14**), on the contrary, claims that in coniferous and hard woods in general there are two periods of growth, one lasting until about the end of May, sinking until the middle of June, and reaching a maximum again in July. Complete cessation resulted by the middle of August. The majority of workers, however, unite with HARTIG in saying that cessation of cambial activity varies greatly with the species concerned.

In the present studies, the latest cuttings in 1909 were made on July 6 upon tree III. At that time growth was still in progress throughout. Comparing these with cuttings taken from the same tree on February 21 of the next year, the following interesting results are obtained. Cutting 2 showed 0.5 of the ring complete, cutting 4, 0.6, cutting 8, 0.85. R. HARTIG (**6**) agrees with T. HARTIG (**8**) that cessation of growth begins first in the crown in trees in open stand and proceeds gradually downward. If such is the case, the data just given present an anomaly, or else growth was accelerated in the apical portions after June 15. However some of HARTIG'S data are in accordance with that already given. For example (BÜSGEN **3**), on June 21 the ring of an oak as compared to that of a previous year gave the following data:

At 1.3 m. height.....0.45 complete
At 3.5 m. height.....0.45 complete
At 5.7 m. height.....0.45 complete
At 7.9 m. height.....0.72 complete
At 12.3 m. height.....0.57 complete
At 14.5 m. height.....0.56 complete (3–4 year branch)

HARTIG then obtained results comparable to the present ones; that is, at about the middle of June he observed that growth was most advanced near the middle of the tree and decreased in both directions from that point. And yet he persists in his assertion that growth ceases in trees in open stand first in the youngest branches. Such being the case, the only possible solution of the data given above is that there must have been a marked acceleration of growth in the apical portions after June 21 and a corresponding decrease in the parts below. Whether the same applies in the pitch pine further investigation must decide. There was an increase in radial growth in the apical shoot and at the same time a decrease below between June 3 and 15, but that growth ceased first above cannot be deduced from the present observations.

As regards the theory advanced by FRIEDRICH concerning two periods of maximum growth in trees, little can be said. The second period if present in *Pinus rigida* must be the minor one, inasmuch as the ring was on an average more than half completed on June 15.

Width of the ring

Measurements were made from sections of tree III to determine the width of the ring at different heights. According to HARTIG, in trees in open stand the amount of wood formed increases from apex to base. This may arise from one of two alternatives; either the annual ring may decrease in size owing to the increasing diameter, or the reverse may be true. The latter, he says, is but rarely the case and sometimes occurs in trees which are exceptionally well nourished, that is, those possessing a large vigorous crown. From these observations it is to be expected that in *Pinus rigida* the ring would increase perceptibly in width toward the base, inasmuch as the crown is as a rule not exceptionally well developed. Such was the case. At cuttings 1 and 4, the completed ring on February 21, 1910, was about the same width. At cutting 8 it was but 0.85 the size of that above, while cutting 12 showed a still further decrease to 0.70. It follows that in *Pinus rigida*, if there is such a decrease in the size of the ring from apex downward in young vigorous growing trees, the same applies with even greater force in older trees with longer axis and poorly developed crown.

The living portion of the cortex, on the contrary, follows a law exactly the reverse. In the upper portions of the crown the cortex is necessarily thin, inasmuch as it contains a relatively small series of bast parenchyma and sieve tube areas. Below, the thickness of the cortex increases markedly, so much so in fact that it often attains 3–5 cm. in width. The storing capacity of the cortex as a result must be greatest in the basal portions of the trunk. Assuming that food abundance alone was concerned in cambial awakening, the latter would result first below. Inasmuch as it does not, there are certainly other determining factors, chief among which is probably insolation.

Investigations on the older trees revealed a number of factors of sufficient interest to demand mention in this paper. A curious feature long known to former workers was especially prevalent. I refer to the often noted lessened density of the wood on the south side of trees. This is due to the fact that the proportion of summer wood on the north side is greater as compared with the width of the ring than on the south side. This disparity in wood formation, however, is not so marked in young individuals. The ring formation is much more regular and it is only in the older trees that the phenomenon above described is seen. As to the cause of this lessened density on the south side, no reasonable conclusion was attained in these investigations, nor has it ever been satisfactorily accounted for. It is without doubt correlated with insolation in some way, but further study is necessary to determine this definitely.

The manner of cambial awakening likewise presents an interesting study. It was observed that even on different sides of the same section a noticeable disparity often occurred. In some cases growth had proceeded to the extent of one or two partly formed tracheids, while in closely neighboring spots the cambium appeared as yet in the resting condition. Nor was one tracheid completely formed as to size before another began. Often rows of three or four small tracheids were visible, none of which had yet attained half the size of those formed first the previous year. In such cases it would appear that cell division was so rapid in the cambial region during favorable seasons that new elements were laid down before

their predecessors had yet attained their maximum size and strength.

Double rings were often in evidence in the old trees. These might easily cause miscalculation as to age. The phenomenon of double ring formation has often been observed, especially in broad-leaved trees. Here it was ascribed sometimes to partial or complete defoliation, at others to favorable or unfavorable external factors. The first assumption would not hold in *Pinus rigida* in this case or in general, since defoliation rarely occurs. The cause must be ascribed to external growth conditions, but what these are would be difficult to determine. That they are most prevalent in old trees is well known, and this would lead one to infer that their formation is in some manner correlated with inhibition of growth, since the effects of this are most marked on older less vigorous individuals.

Secondary thickening in the roots

Little stress was put on the study of secondary root thickening in the present investigation. Only one cutting was taken, on April 27, 1910, for purposes of comparison, so that no reliable deductions can be made. At this time cambial activity was not manifest, although it must have been in process throughout the aerial portion with the possible exception of the apical shoot. T. HARTIG (8) claimed that cambial awakening in the roots is much later than in the aerial portions. He gave midsummer as the time of first inception and said it continued far into October. Whether the same applies to *Pinus rigida* further investigation only can decide. Suffice it to say, however, that the growth in thickness of roots must not be confused with growth in length. The latter is manifest often as early as March and continues throughout the season.

Summary

1. The histological characters of *Pinus rigida* present no wide variation from the normal coniferous type.

2. The secondary thickening in the root is similar to that in the stem, but differs (*a*) in less sharp demarcation between the annual rings, (*b*) in the biseriate character of tracheids, and (*c*) in less density.

3. Growth began in young 20–30-year old specimens of *Pinus rigida* in the vicinity of Ithaca as early as April 15. While there was no direct evidence of cambial awakening secured the previous year, sections taken at a later date showed growth in such an advanced state that it must have begun fully as early.

4. In older trees cambial awakening is sometimes retarded at the base where proper insolation is lacking.

5. There is no appreciable difference in the time of cambial awakening on the north and south sides of trees.

6. Growth began first in 20–25-year-old specimens at some distance below the apical shoot, but during a period of 19 days gradually spread upward until it reached the apex of the trees.

7. Investigations on trees *A*, *B*, and *C* tend to show that growth in older individuals begins first in the crown and spreads downward. The time of its inception at the base varies with conditions of insolation, bark, etc.

8. Growth in the branches follows the same rule as in the main axis. The time of awakening in the former is almost if not absolutely identical with that in the latter.

9. Growth spreads down the main axis faster than it does along the lateral shoots.

10. Except in the terminal shoot, growth in diameter was more rapid between May 25 and June 6. In the terminal shoot itself greatest rapidity of growth was manifested between June 6 and June 15.

11. No reliable deductions concerning cessation of cambial activity can be drawn from the present investigations.

12. The width of the complete ring decreases from apex to base; the living portion of the cortex follows the reverse rule.

13. A number of peculiarities already noted by others are prevalent in mature specimens. These are (*a*) lessened density of wood on the south side of trees, (*b*) irregularity of cambial awakening in closely neighboring parts of the same section, (*c*) successive formation of new elements before previous ones have reached their maximum size, and (*d*) double rings.

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EXPLANATION OF PLATES XXIV AND XXV

FIG. 1.—Cutting taken from apical shoot of tree III April 15, 1910; cambium in the resting condition; ×50.

FIG. 2.—Same, but cutting taken about 1 m. from the apex; cambium in the resting condition; ×50.

FIG. 3.—Same, but cutting taken about 2 m. from the apex; growth in evidence to the extent of one or two partly formed tracheids; ×50.

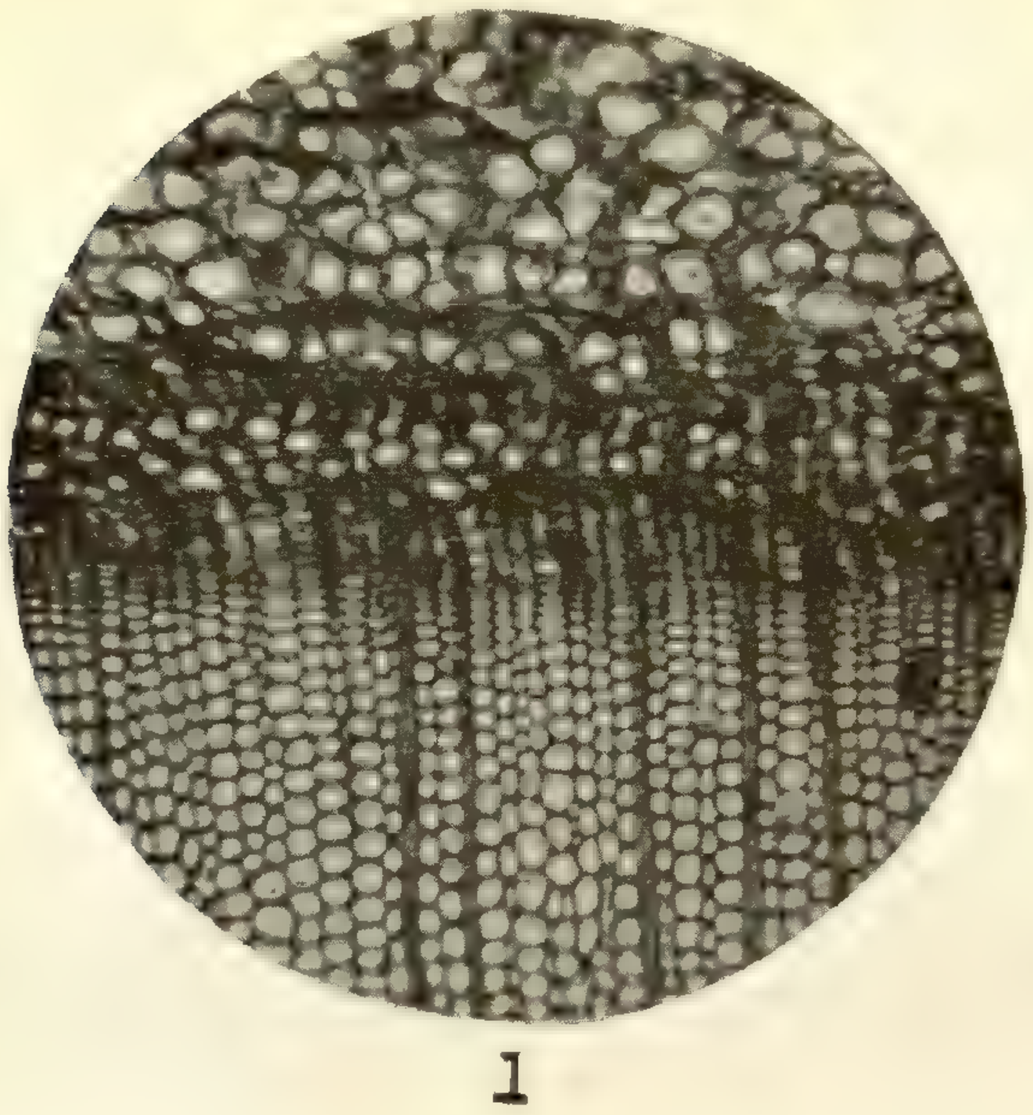
FIG. 4.—Cutting taken from apical shoot of tree III May 4, 1910; growth just beginning at *A;* compare with fig. 1; ×50.

FIG. 5.—Same, but cutting taken 1 m. from the apex; growth slightly more advanced; compare with fig. 2; ×50.

FIG. 6.—Same, but cutting taken from the apex; growth in evidence to the amount of 3 or 4 tracheids; compare with fig. 3; ×50.

FIG. 7.—Cutting taken from tree III April 15, 1910, about 3 m. from the apex; growth in evidence to the extent of one or two partly formed tracheids; ×50.

FIG. 8.—Same, but cutting taken about 4 m. from the apex; growth in evidence to about the same extent as in fig. 7; ×50.



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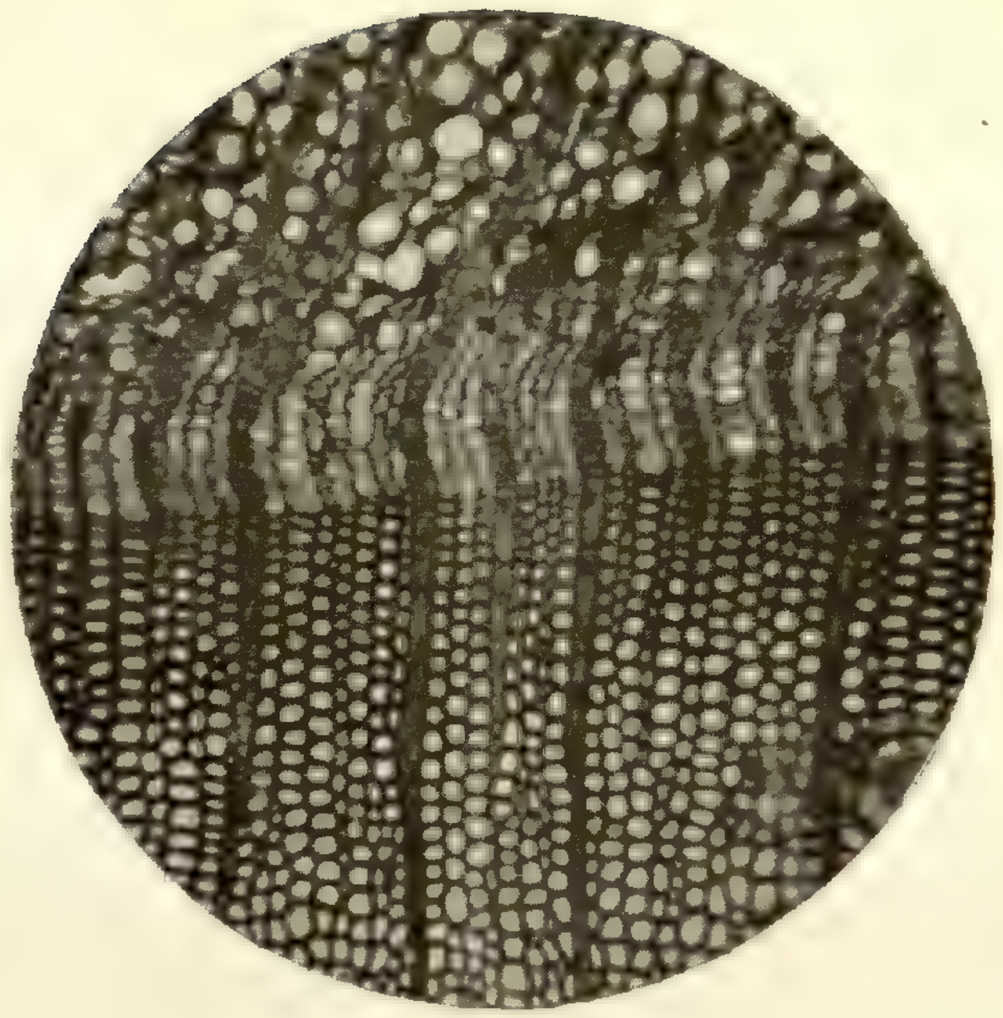

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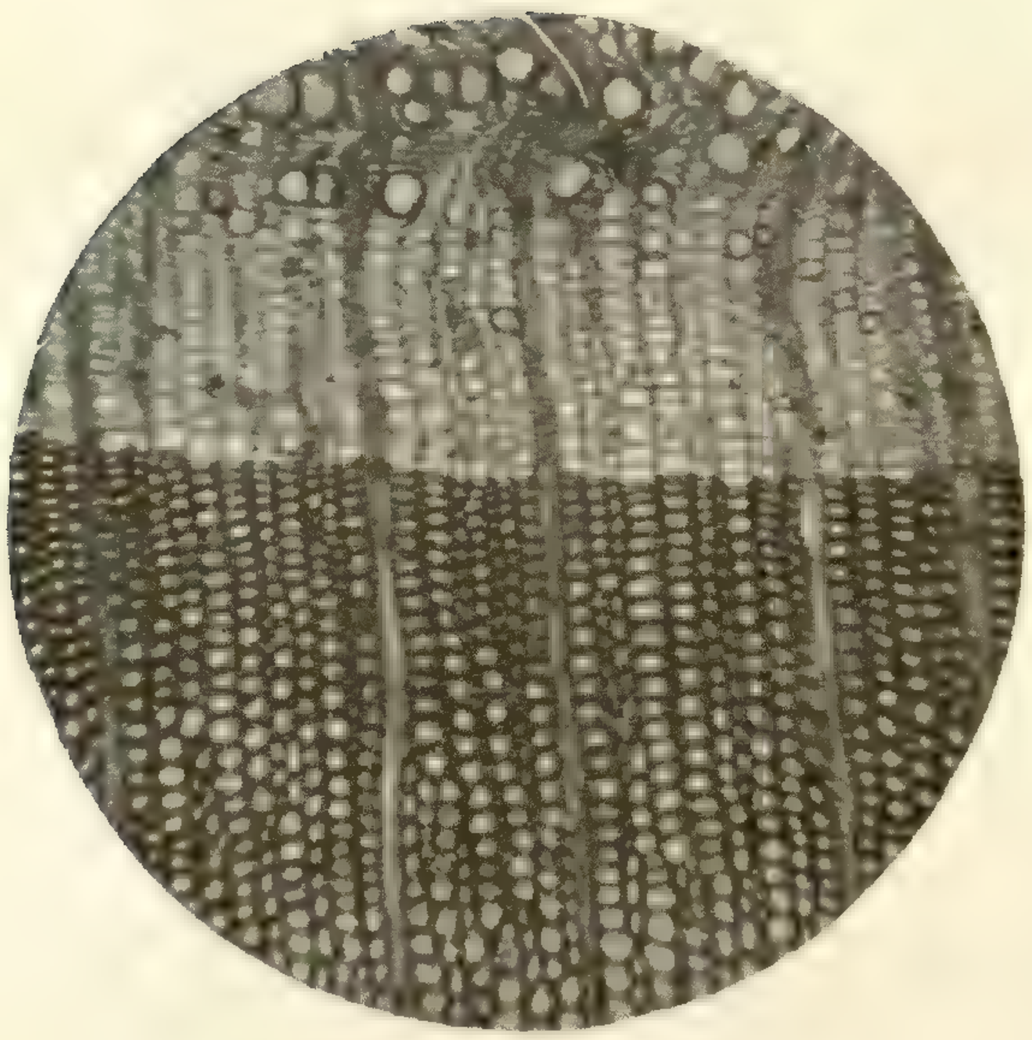

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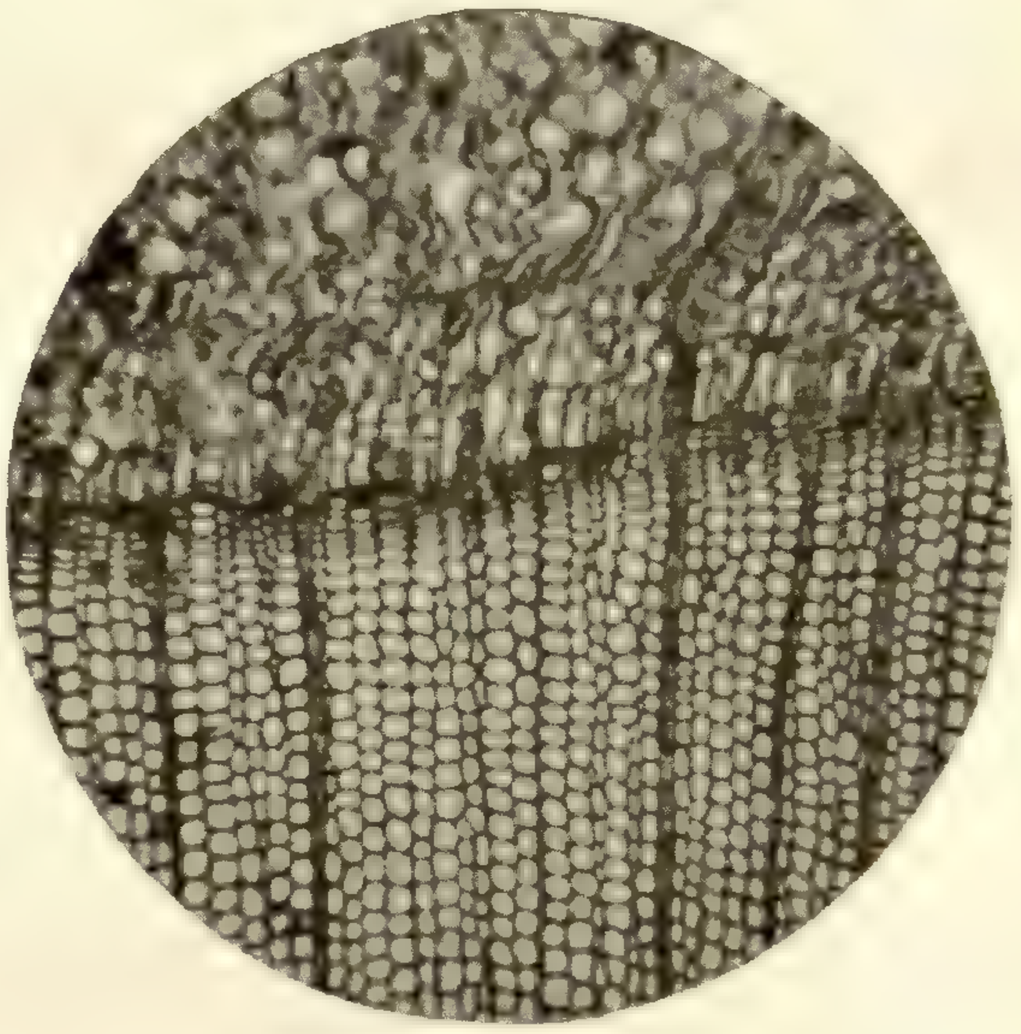

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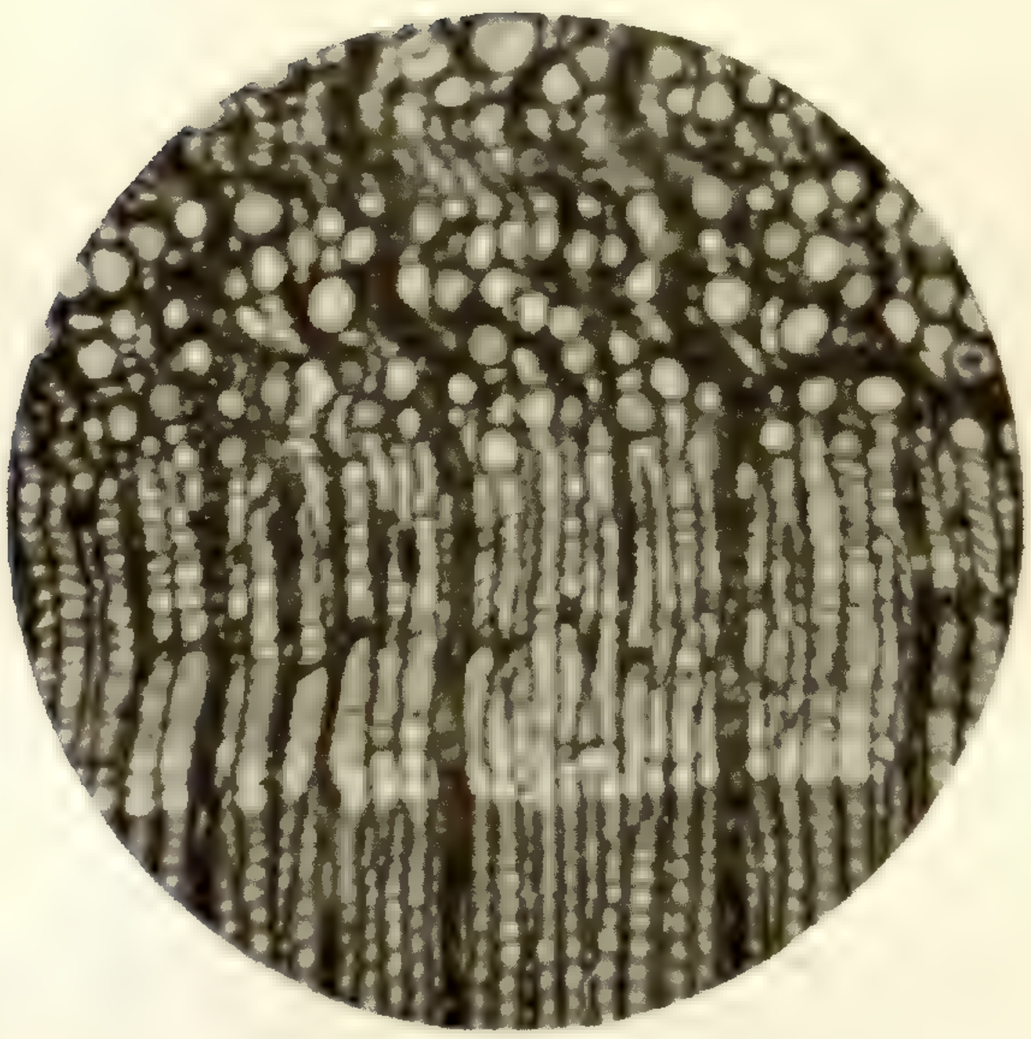

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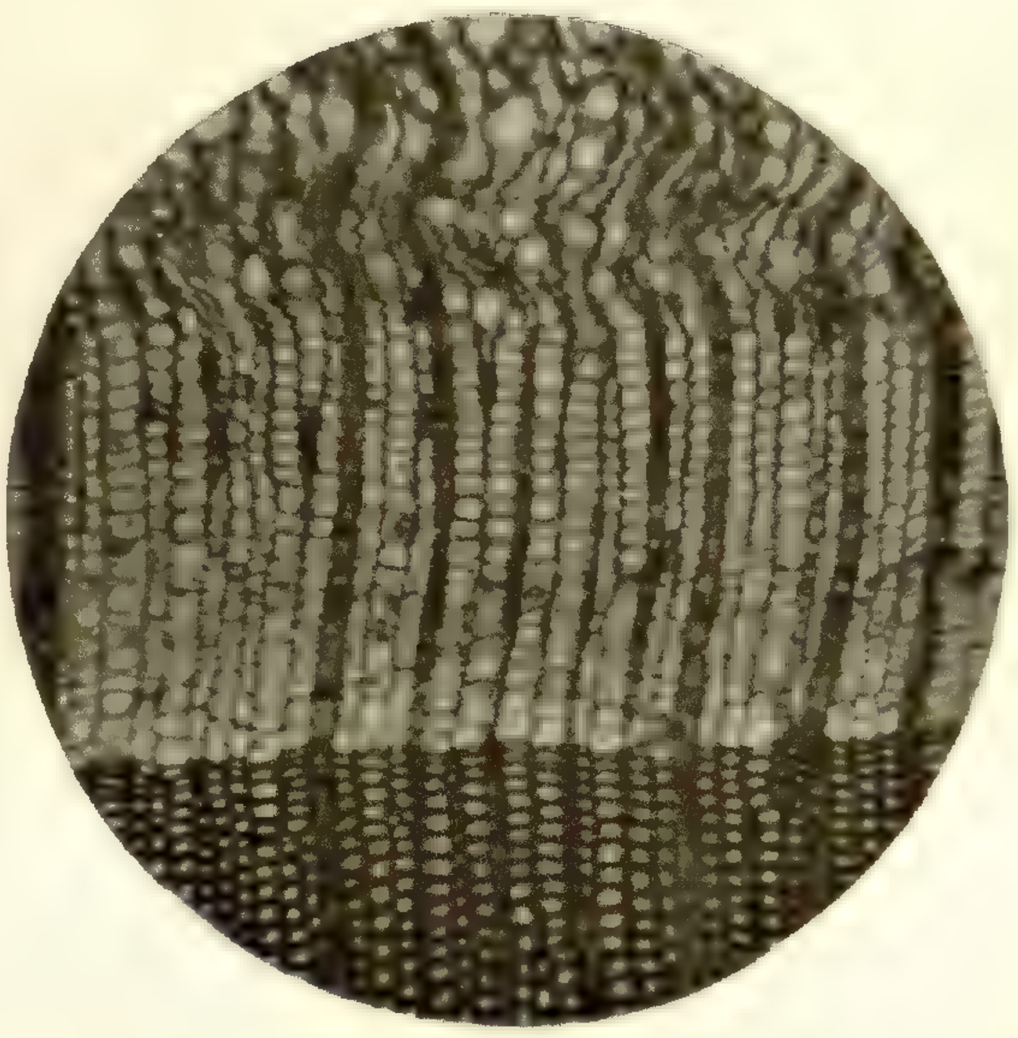

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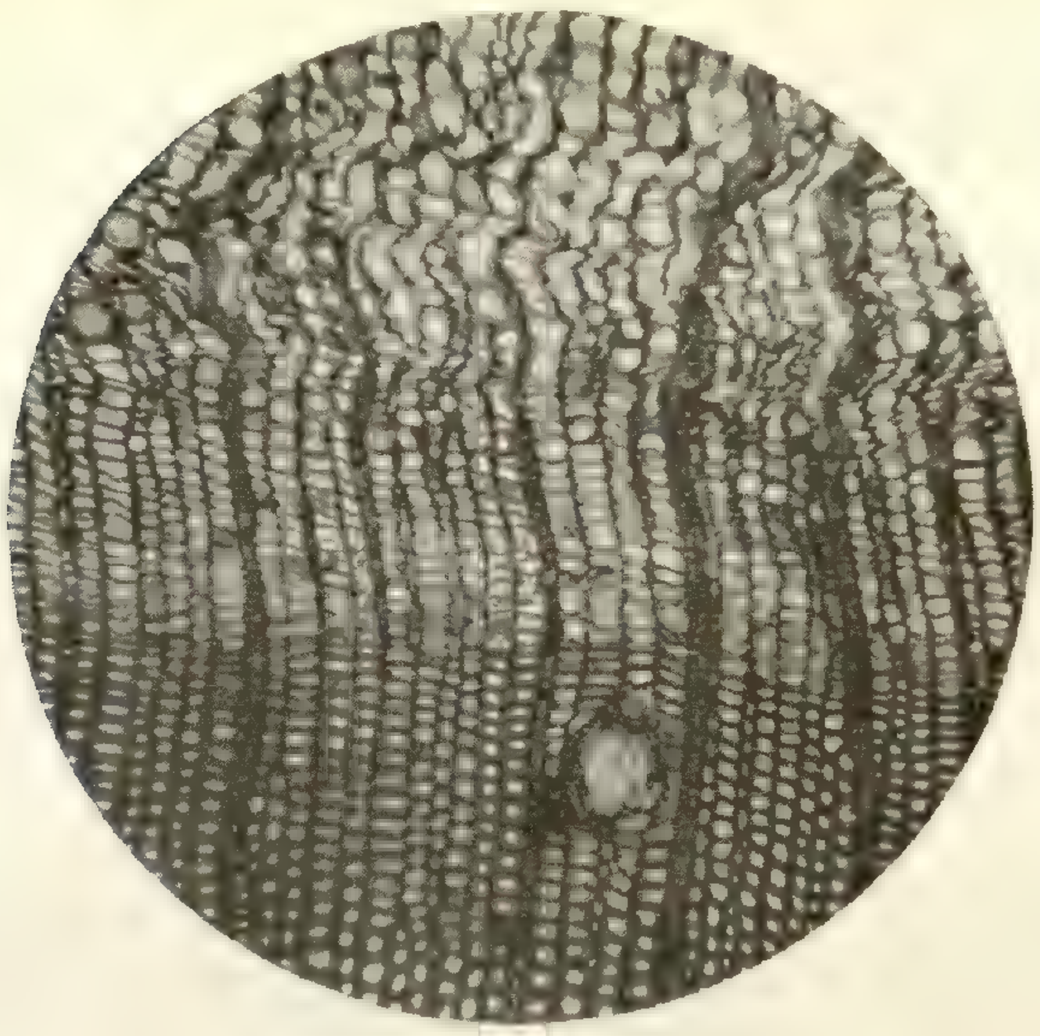
BROWN on PINUS RIGIDA



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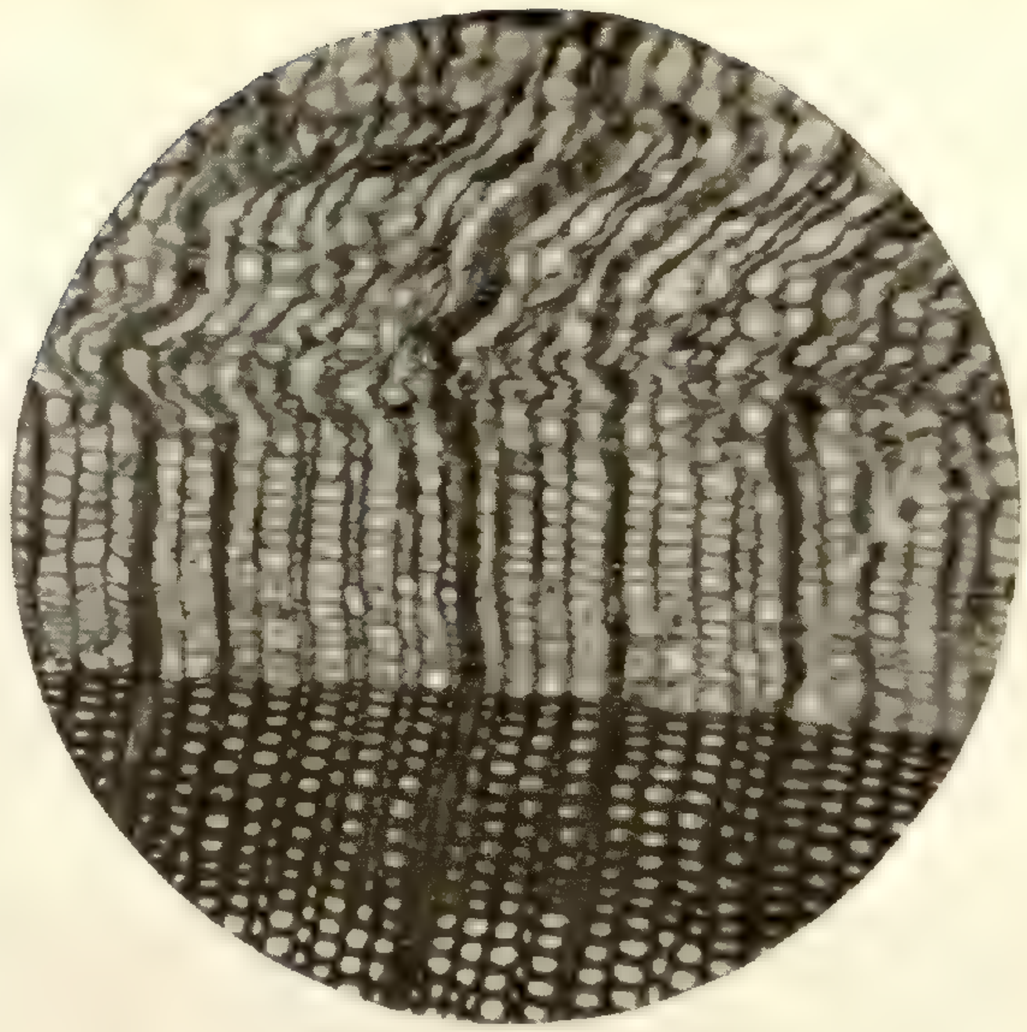

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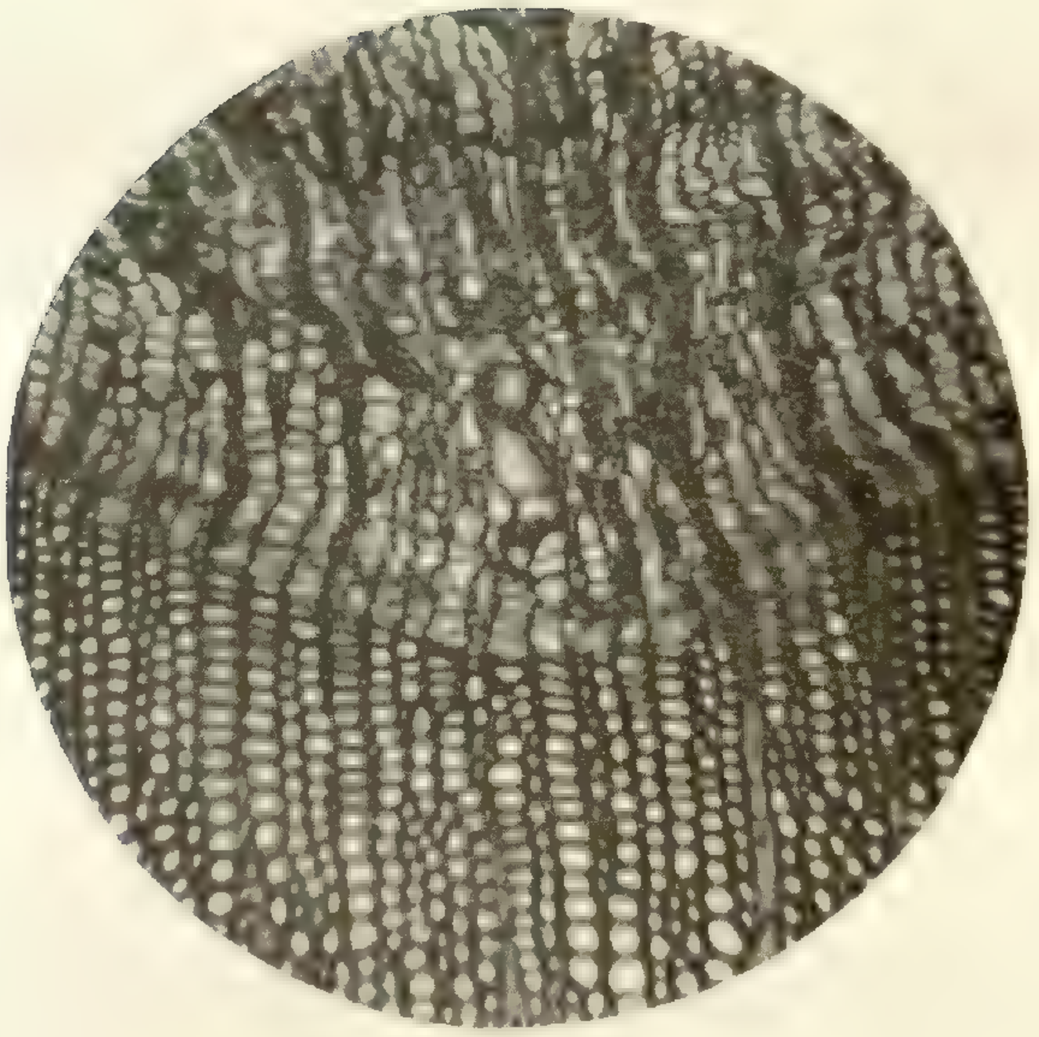

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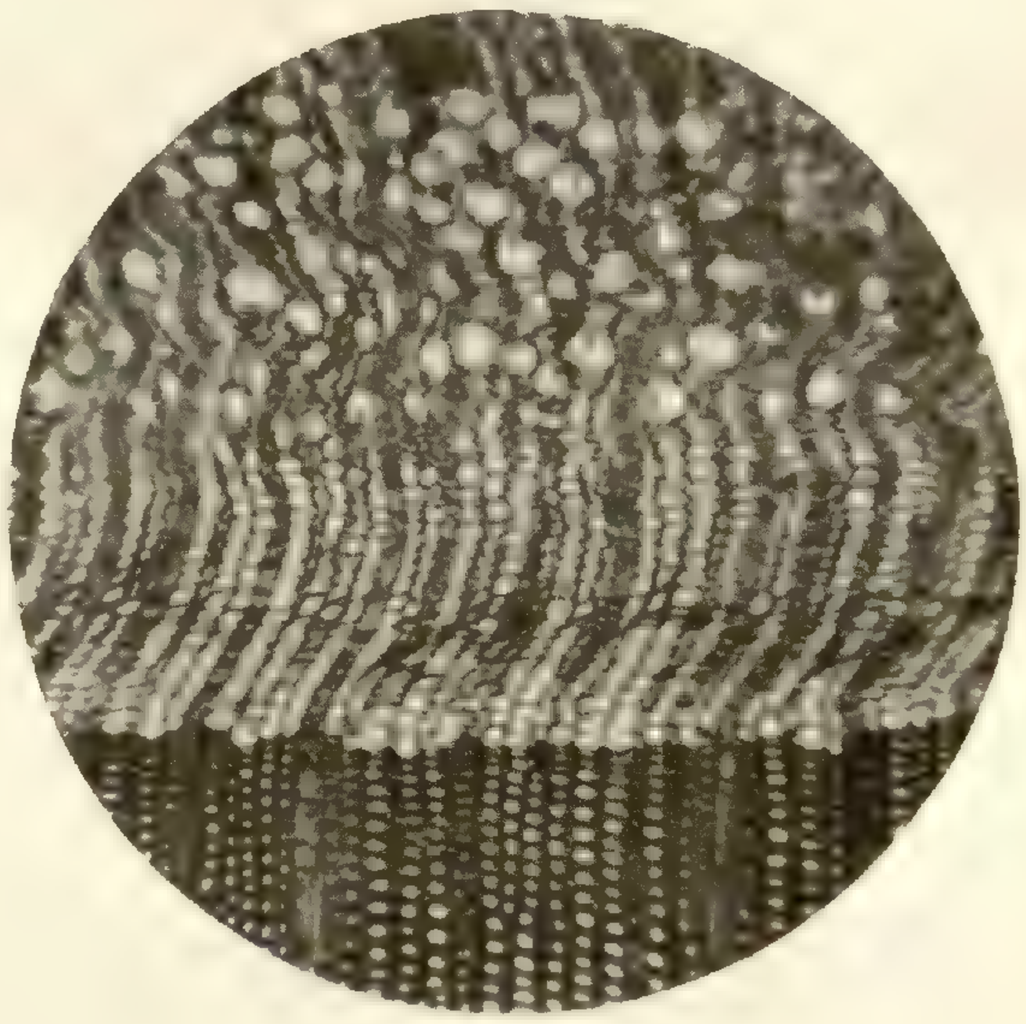

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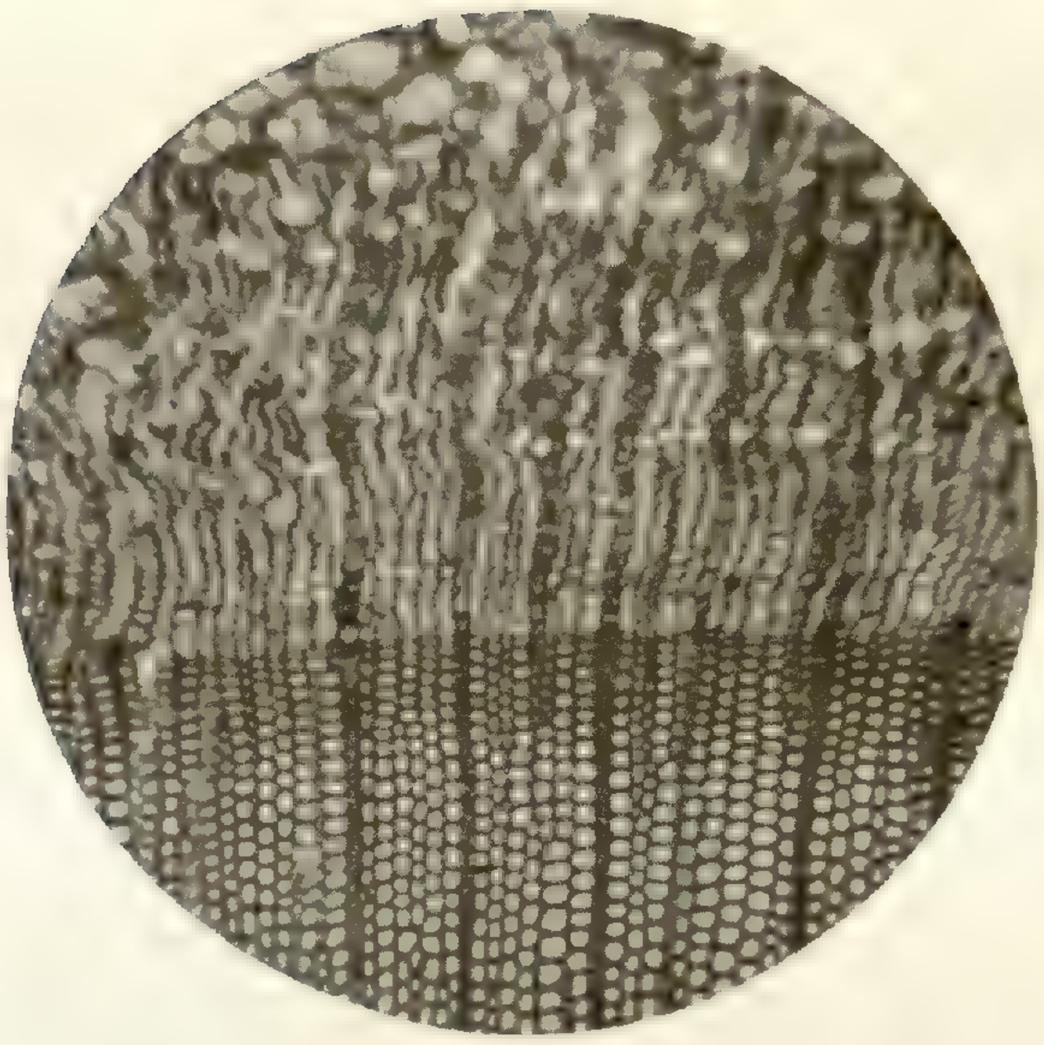

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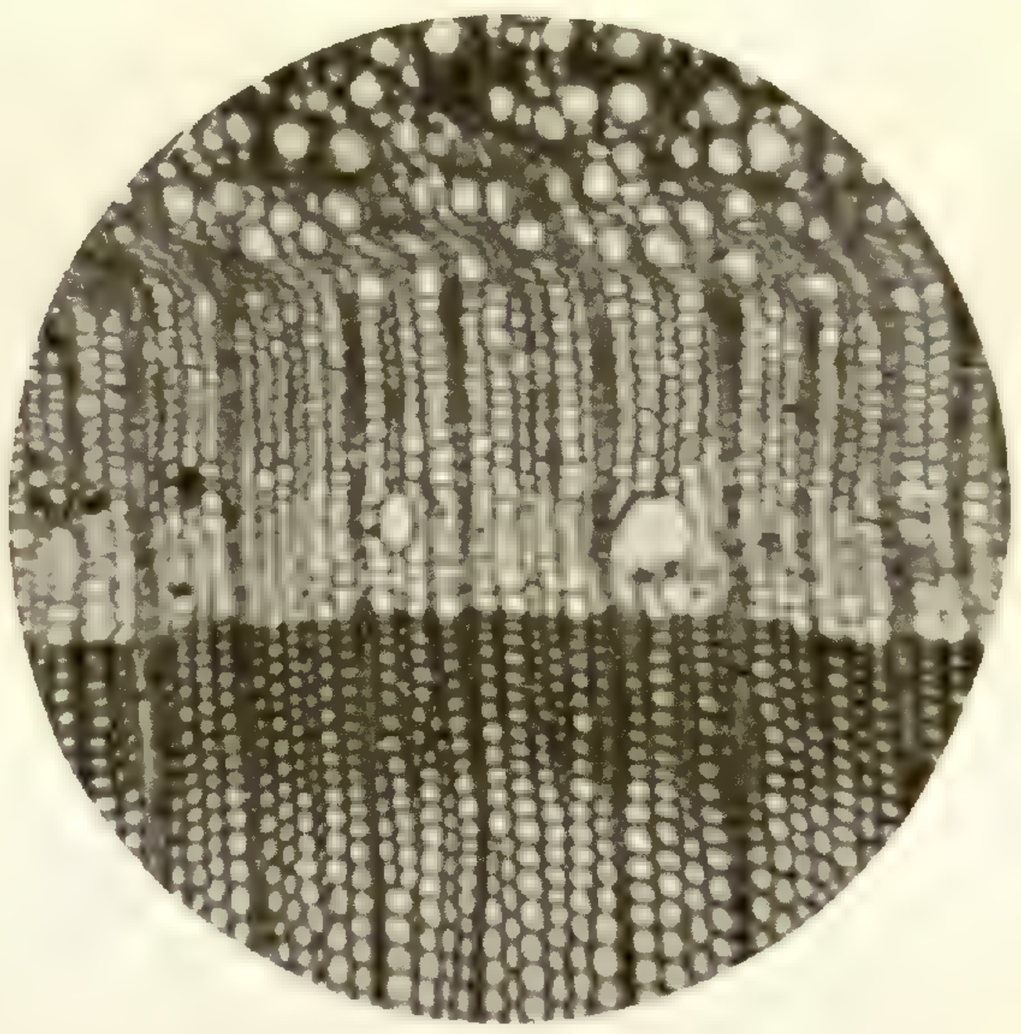

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BROWN on PINUS RIGIDA

FIG. 9.—Same, but cutting taken about 5 m. from the apex; cambium in the resting condition; ×50.

FIG. 10.—Cutting from main axis of tree VI April 22, 1910, at a distance of 3 m. from the apex; growth in evidence to the extent of several rows of partially formed tracheids; ×50.

FIG. 11.—Same, but cutting from the base of a lateral branch which entered the main axis 20 cm. below cutting shown in fig. 10; no growth in evidence; ×50.

FIG. 12.—Same, but cutting taken 40 cm. below that in fig. 10; growth in evidence to the extent of several rows of tracheids; ×50.

CONTRIBUTIONS FROM THE ROCKY MOUNTAIN HERBARIUM. XII

NEW PLANTS FROM IDAHO

AVEN NELSON

In this paper are continued the studies upon the plants of southern and western Idaho, begun in no. IX of this series of Contributions. As stated in the preceding paper, the present studies are based upon collections made in 1911, largely by Mr. J. FRANCIS MACBRIDE, but assisted in the field for a time by the writer. There are also included in this paper a few species based upon collections made by Miss JUNE A. CLARK, of Boise, at present a student in the Idaho State University. During 1911 she made very creditable collections of the plants of the mountains adjacent to Boise, and in the mountains of Washington County of her state.

Melica Macbridei V. H. Rowland, n. sp.—A green slender erect tufted perennial, 2–5 dm. high, growing from bulbs, which may be solitary or in clusters of 2–6: culms and sheaths (which exceed the internodes) hispid-scabrous on the prominent nerves: leaves exceeding the sheaths in length, usually 3 in number, the basal withering early, flat, thin, and weakly ascending, 1–4 mm. wide: panicle loosely open; rachis decreasingly scabrous toward the apex, with 3–9 nodes, the first internode 3.5–5 cm. long: rays 1–3 at each node of the rachis, if 3, the first subsessile, the second on a short pedicel, the third on a long capillary reflexed pedicel: spikelets 2–5-flowered, 7–13 mm. long, with terminal flower sterile, never flattened: glumes unequal, herbaceous, scarious-margined, quite often purple-tipped, oblong, acute; the first 4 mm. long, 3-nerved and about two-thirds as long as the second; the second 5-nerved, 6 mm. long: lemma thicker than and about equaling the second glume, lightly scabrous throughout, obtusely bifid: palet reaching to the notch in the lemma, 2-keeled, spathe-shaped with the lower part inclosing the white wormlike rachilla, ciliate on the keels from near the middle to the apex: fruit cylindrical with the divergent styles sometimes persistent.

This species is nearest to *Melica bromoides* Gray, from which it differs as follows: *M. Macbridei* is about one-half as high as *M. bromoides* and much slenderer and more graceful in appearance; it is much more scabrous and the roughness continues beneath the sheaths to very near the nodes of the culm; the sheaths exceed the internodes; the floral parts are shorter and wider than in *M. bromoides;* the nerves of the glumes and lemmas never extend to the margins; and lastly the rachilla between the flowers is smooth, white, and "wormlike" and never green as in the other.

This is number 948 of MACBRIDE'S 1911 collection of Idaho plants, secured on dry slopes at Silver City, June 20.

Calochortus umbellatus, n. sp.—Bulb small, ovoid to subglobose: stems slender, 3–5 dm. high, 2–3-leaved; lower leaf long, 4–8 mm. wide, from one-half to three-fourths as long as the stem; the other leaves narrowly linear (if only one, near the middle), 5–10 cm. long: flowers 3–9, in an umbel; pedicels slender, erect (in a fascicle), 5–10 cm. long; involucral bracts few–several, 2–4 cm. long, the ovate base scarious, abruptly narrowed to the long filiform green acumination: sepals lanceolate, acuminate, one margin more broadly scarious than the other, 25 mm. or less long: petals obovate-cuneate, the rounded summit more or less erose and abruptly apiculate or subacute, white, with an indigo or purple spot near the middle; the gland small, round, yellow, short-setose, some long soft filamentous hairs scattered over the lower half of the petal: filaments not much if any longer than the anthers, dilating gradually from apex to base: capsule ellipsoidal, about 15 mm. long, narrowly thin-winged, lightly transversely striate.

There is no doubt that this has passed as *C. nitidus* Dougl., to which it is closely related. The Idaho specimens seen by the writer cannot, however, well be so referred. PURDY has recharacterized *C. nitidus* in his excellent revision (Proc. Cal. Acad. Sci. III. **2**:128. 1901) and the following facts, drawn from his description are in direct contrast with *C. umbellatus:* "Stems *bulb-bearing* near base, *not* bracted in the middle"; "umbel of 2–4 flowers subtended by *2–4* linear bracts"; "sepals *ovate-lanceolate, exceeding* the petals"; "petals *2 inches* long, the *same* in width"; "filaments *filiform*, winged *below*"; capsule strongly winged and *crested.*"

NELSON and MACBRIDE'S no. 1197, July 19, 1911, is taken as the type. The species seemed quite abundant on sagebrush lands near Wood River at Ketchum. Mr. C. N. WOODS has also secured it (no. 258) in the same county (Blaine). A specimen from Yellowstone Park by Mrs. E. W. SCHEUBER is also referable here.

Zygadenus salinus, n. sp.—Bulbs globose, or even depressed globose, not deep-set (4–8 cm.), 1–3 cm. in diameter; outer bulb-coats brown, thin, and fragile; the next succeeding ones delicately thin-scarious, glistening white: leaves green, grasslike, usually folded, scabrous on the margins, somewhat pruinose, especially on the greenish sheaths, 7–12 mm. broad, shorter than the scapose stems: stems slender, erect, 3–6 dm. high, with 2–3 non-sheathing linear leaves: raceme short, rather crowded; the pedicels slender, becoming 2–3 cm. long; the bracts with short ovate base and very long linear acumination, the lower as long as or longer than the pedicels: flowers in a simple raceme, yellowish-white; perianth segments nearly similar, 3–7-nerved, all clawed; the sepals with very short claw, ovate, obtuse; the petals elliptic, obtuse, with evident claw which is more or less concave or inrolled; the glands in both small, inconspicuous, and confined almost wholly to the upper part of the claw: stamens surpassing the perianth, on filaments only slightly dilated below: ovary free from the calyx; the styles 2–3 mm. long: fruit ovate, about 6 mm. long; the cells united to the summit.

I should hesitate to describe this as a new species were it not for the globose bulbs and the habitat. The near allies are *Z. venenosus* Wats. and *Z. intermedius* Rydb. These have elongated bulbs; the former has conspicuous glands, and the latter has all the leaves with scarious sheathing base. Both have deep-set bulbs, and belong to dry non-saline soil, while the proposed species was secured in alkali-bog lands, with the bulb but a few centimeters below the surface. It seems that typical *Z. venenosus* is confined to the coast states (see PIPER's Fl. Wash. 198, and BLANKINSHIP, Mont. Science Studies 1:45).

Type no. 889, MACBRIDE, Emmett, June 9, 1911.

Salix boiseana, n. sp.—A low shrub, forming clumps, 1–2 m. high: twigs glabrous, reddish brown or chestnut, slightly shining or obscurely glaucous: leaves oblong, either obtuse or subacute at apex, usually cuneately narrowed at base, 2–4 cm. long, minutely pubescent but green above, pale with a fine tomentum beneath, margin quite entire; stipules wanting: pistillate aments with two or three foliar bracts at base, 3–5 cm. long: floral bracts (scales) small, ovate, obtuse and brown, about half as long as the pedicels, long silky hairy below, especially near the apex and margin, gla-

brate above: pedicels slender, 1.5–2 mm. long; capsules glabrous, 3–4 mm. long: style evident but very short (less than 0.5 mm.).

This is most nearly allied to *S. Wolfii* Bebb, but seems to be distinct by the cuneate base of the leaves, which are glabrous or nearly so above, tomentose on the lower face (not silky-villous with shining hairs on both sides), by the longer pedicels, the slenderly virgate fertile stems (*S. Wolfii* is freely short-branched), and the longer fertile aments. *S. boiseana* belongs to lower altitudes and matures much earlier in the season.

Miss JUNE CLARK secured the type material (no. 48) in overripe condition, May 29, 1911, near Boise at an altitude of less than 3000 feet.

Eriogonum fasciculifolium, n. sp.—The shrubby base low (1–2 dm.) and somewhat di- or trichotomously branched; the more or less scaly bark dark brown or dirty black: leaves fasciculate or verticillate on the enlarged nodes, mostly on the crownlike apex of the branchlets, linear or narrowly oblanceolate, 1–3 cm. long, tapering to a short petiole, rather thick, pale-green, glabrate above, obscurely tomentose below: peduncles from the upper nodes or terminal, 4–8 cm. long, bearing a few-rayed umbel, lightly pubescent; the bracts foliar, apparently always few (2–4), or sometimes wanting: rays 12–20 mm. long: involucre many-flowered, campanulate, its ovate-oblong reflexed lobes as long as the tube, sparsely silky-villous: flowers pale yellowish-white, rather large: sepals similar, broadly obovate, about 5 mm. long, lightly silky-villous below and on the pedicel to the joint: filaments pubescent below, much shorter than the triangular glabrous achene.

This new member of § PSEUDO-UMBELLATA is at once distinguished by its branched shrubby base and its very narrow leaves, though it has all of the characteristics of the section.

A limited quantity only was secured by Miss JUNE CLARK at Tamarack, Washington County, Idaho, August 12, 1911, no. 236, on a dry mountain side.

Stellaria (ALSINE) **praecox,** n. sp.—A diminutive vernal species of arid districts: stems usually simple but sometimes branched from the base, glabrous except for some crisped hairs on the lower internodes, 7–15 cm. high (including the long filiform pedicels): leaves few, mostly in a basal rosette, with 1 or 2 pairs on the lower part of the nearly filiform stem, narrowly lance-linear, 5–12 mm. long: cyme unequally 3-rayed, some of the rays again unequally trichotomous; the bracts minute, somewhat scarious: sepals

lanceolate, scarious-margined, about 3–5 mm. long: petals wanting: stamens 5, opposite the sepals and less than half as long: stigmas 3, nearly sessile: capsule ellipsoidal, each of its 3 valves 2-toothed, shorter than the calyx; seeds several.

Some of its characters are suggestive of *S. umbellata* Turcz. (*Alsine baicalensis* Coville). That also is apetalous and has five stamens, but in it they alternate with the sepals. The capsule is oblong-ovoid and twice as long as the sepals. The seeds in the two seem nearly identical, with an almost annular embryo. The aspect of the two species of course is wholly different, *S. praecox* looking more like a very slender *S. longipes* Goldie.

The plant has added interest because many of the scarcely distorted capsules were found to be filled with a smut which Dr. CLINTON pronounces as new also, and to which he has given the name *Ustilago Stellariae.*

MACBRIDE secured this at Falk's Store, Canyon County, Idaho, on moist slopes, under sagebrush, no. 763, April 24, 1911.

Crataegus tennowana, n. sp.—Small treelike shrubs, 3–6 m. high, sometimes growing in clumps and then lower and less treelike: trunk short, usually less than 1 dm. in diameter: spines straight, nearly at right angles, lustrous reddish-brown becoming grayish, about 15 mm. long (1–2 cm.): leaves mostly oval (varying to suborbicular) in general outline, both base and apex with rounded contour, often however cuneately narrowed below and more rarely above as well; the upper half from shallowly to deeply and irregularly serrate, the teeth with more or fewer gland-tipped serrulations; the lower half glandular serrulate or with a few sessile glands on the entire margins (occasionally the glands extend down upon the petiole which is only 2–10 mm. long); pubescence wanting from the first upon the petioles and on the underside of the leaves, sparsely and minutely hirsute on the upper side, especially along the veins, from the first to maturity; the veins of the rather thin leaves somewhat superficial on the lower side, the midrib flattened and narrowly wing-margined, at least in the young leaves: corymb wholly glabrous except for a slight pubescence on the inner face of the calyx lobes, 5–15-flowered, with scattering glands on the peduncle and pedicels and very rarely on the triangular-lanceolate persistent calyx lobes: stamens seemingly 8 when the styles and carpels are 4, and 10 when the styles and

carpels are 5 (the more unusual number); anthers pink: fruit black or purplish-black, maturing in July: carpels with rounded back, cuneately narrowed to the somewhat sulcate ventral angle, not narrowed at base.

This may be thought too near *C. Douglasii* Lindl., but authors are fairly well agreed that that species should have the following characters, to none of which this seems to attain:

Tree size (30–40 feet high, with trunk sometimes as much as 20 inches in diameter): leaves ovate to obovate, with cuneate base, densely pubescent above, on the veins below, and on the petioles when young: calyx lobes deciduous, glandular serrate: stamens 20 (SARGENT), 10–20 (BRITTON, ROBINSON, and FERNALD, *et al.*): anthers yellow: styles surrounded at the base with long pale hairs: fruit ripening in August and September: carpels narrowed at base.

In view of the differences indicated it would seem that at least some of the western forms that have heretofore passed as *C. Douglasii* need to be separated from it.

The type is MACBRIDE'S no. 799 (flowers, May 10; ripe fruit, from naked tree, July 8), moist woods, Falk's Store, Canyon County.

Trifolium tropicum, n. sp.—Apparently green and glabrous but under a lens pubescent with scattering white hairs, especially near the midrib both above and below: stems single, from slender rootstocks, erect, slender, 2–3 dm. high: leaflets linear, 3–6 cm. long, 2–5 mm. wide, minutely denticulate by the projection of the beautifully arcuate nerves; petioles slender, from much shorter to much longer than the leaflets; stipules linear, the free portion usually denticulate, 14–18 mm. long, either shorter or longer than the adnate portions: heads about 2 cm. high, nearly as broad, solitary or 1 or 2 smaller ones from the upper leaf-axils, in bud silvery-silky with the long abundant hairs on the filiform calyx lobes: flowers purple to rose-red, soon reflexed and nearly concealing the pubescence of the calyx: calyx lobes longer than the thin scarious glabrate tube: standard oblong, with rounded apiculate apex, about 10 mm. long and 4 mm. broad when spread out flat; wings as long as the standard, the blade narrowly oblong, conspicuously auricled at base, as long as the slender claw; keel petals semi-oval, shorter than the wings, the claw longer than the blade: style a little longer than the stamens: ovary glabrous, about 8-ovuled.

Most nearly allied to *T. Harneyensis* Howell, from which it is at once separated by its pubescent leaves, sessile flowers (which are early, not tardily, reflexed), and glabrous calyx tube and ovary.

MACBRIDE'S no. 967, from Jordan Valley, Owyhee County, in moist loam soil, June 22, 1911, is the type.

Lupinus tenuispicus, n. sp.—Silvery-silky, with loose, copious, somewhat spreading and tangled hairs: perennial, in dense clumps on a woody caudex, 3–7 dm. high: stems rather slender, sparingly branched: radical leaves on slender petioles 1–2 dm. long; leaflets 6–9, narrowly oblanceolate or nearly linear, 4–6 cm. long; cauline leaves similar, shorter-petioled and (above) sessile: spikes slender, crowded, 5–15 cm. long: bracts small, linear-lanceolate, somewhat shorter than the nearly sessile calyx: calyx barely gibbous at base, about 5 mm. long: flowers blue: standard nearly orbicular, the blade pubescent on the back with fine long hairs (only visible under a good lens), 6–8 mm. long, sharply emarginate at apex; wing petals oval, on very short claws; keel petals small and deli-cate, the blade semi-ovate, on a claw half as long: pods very short, 1–3-seeded, pubescence as on the rest of the plant.

I can find no described species in this range having the very slender and crowded spikes, the small apparently glabrous petals, and the short few-seeded (often only one) pods of this form.

No. 203, by Miss JUNE CLARK, from Tamarack, in the mountains of Washington County, Idaho, August 8, 1911, is the type.

Astragalus nudisiliquus, n. sp.—Habit and appearance of *A. utahensis* T. & G., the white indument even thicker and more felted: caudex woody and freely branched: pod about 20 mm. long, probably at first white woolly-hirsute, the indument at length deciduous and disclosing the longitudinal striae, coriaceous-woody, ovoid, flattened dorsally, the acute apex abruptly flexed, the dorsal suture slightly keeled, the ventral somewhat sulcate.

When the writer collected this and first examined it later, he took it for granted that it was merely an over mature *A. utahensis*. On noting the character of the pod, however, it is evident that this is not the case. In that species the indument is permanent, both sutures are inflexed, the body of the pod is smaller, the apex is essentially straight, and, as a more strikingly characteristic difference, the striae are transverse. In view of these facts it seems best to put this species (which has no doubt passed for *A. utahensis*) on record.

Secured by NELSON and MACBRIDE on the steep cobblestone bluffs of the Snake River, at King Hill, Idaho, July 15, 1911, no 1088.

Astragalus obfalcatus, n. sp.—The woody taproot vertical, with an enlarged crown, or in older plants with closely branched caudex, the branches with enlarged crowns: stems solitary or few from the crown or crowns, stoutish, erect, coarsely striate, green and glabrate or sparsely hirsute with white hairs, few-leaved, 1–3 dm. high: leaves crowded on the crowns, somewhat spreading upon the nearly erect petioles (the dead petioles persisting), canescent with straight stiffish widely spreading coarse hairs; leaflets 7–13, from oblong (or spatulate) to elliptic or obovate, 10–20 mm. long; petioles 5–10 cm. long, those of the stem shorter: peduncles axillary, few-flowered: calyx tube 5–7 mm. long, the pubescence on it mostly finer and shorter, black in part, its linear lobes nearly as long as its tube: bracts linear, rarely as long as the calyx tube: pods widely divaricate, falcate upward, abruptly long-cuspidate, canescent with coarse hairs, completely 2-celled by the intrusion of the dorsal suture, the rounded back scarcely sulcate, somewhat flattened laterally to the almost carinate ventral edge, the stout stipe not as long as the calyx tube: seeds many.

In habit this species suggests *A. mollissimus* Torr. The shape of the leaflets and even the pubescence is somewhat similar, and the pod is 2-celled, but there the similarity ends. There are a few other species in which the pods are falcate upward, but *A. obfalcatus* approaches none of these as closely as it does *A. mollissimus*.

Secured by MACBRIDE (no. 1023) in dry lava soil, on Reynolds Creek, in Owyhee County, July 3, 1911 (full fruit; flowers not seen), and by NELSON and MACBRIDE (no. 1119), at King Hill, in loose lava cinders, July 15, 1911.

Lathyrus Bradfieldianus, n. sp.—Glabrous, mostly less than 1 m. high, stems weakly erect, among undershrub which give partial support, rather strongly striate but noticeably angled only on the more or less branched upper portion: leaflets mostly 10, subsessile, beautifully and rather strongly veined, bright green above, scarcely paler beneath, from broadly elliptic and obtuse (or even retuse) to narrowly ovate and acute, all subulate-tipped, 15–30 mm. long; tendrils well developed, somewhat branched; rachis moderately stout, the petiolar part usually shorter than the

internodes; stipules large, consisting of a triangular-lanceolate upper portion (which is entire and acute, or somewhat acuminate) and a much larger somewhat reniformly expanded basal part (which is usually coarsely and irregularly 3–5-toothed): flowers large, 3–8, closely approximated at the end of the long (10–15 cm.) axillary peduncles: calyx very oblique, the lanceolate teeth small, each shorter than the part of the tube to which it is attached, except the lower one which is linear and nearly as long as the tube: petals dark blue or purplish, lighter toward the base; the claw of the standard rather broad, sulcately folded and with conspicuous winglike crests at junction with abruptly flexed or reflexed reniform or orbicular emarginate blade; wings broadly elliptic, on a very slender claw shorter than the blade: pods nearly straight, 5–6 cm. or more long, 6–8 mm. broad, about 15-ovuled.

Resembling and related to *L. pauciflorus* Fernald, BOT. GAZ. **19**:335, 1894, from which it is readily distinguished by its broad obtuse lower leaflets, its stipules with their remarkably expanded bases, its more numerous and larger and broader flowers, and always by the conspicuous rounded crownlike crests at the summit of the folded claw.

MACBRIDE'S no. 927, from Silver City, on brush covered hills, June 19, 1911, is the type. Mr. WILLIAM C. CUSICK'S no. 2538, from mountains near North Pine Creek, Oregon, is to be referred here, as well as Miss CLARK'S no. 85, from Boise (Clear Creek), July 4, 1911. The species is named in honor of Mr. A. D. BRADFIELD, superintendent of the Silver City schools, an appreciative student of his local flora, who spent much time in the field assisting Mr. MACBRIDE.

Viola Clarkae, n. sp.—Perennial from a woody sub-horizontal rather long rootstock, which bears a simple or branched caudex: branches of the caudex 1–4 cm. long, brown, and rough with the old petiolar bases: new plants often arising from the nodes of the rootstock at intervals of 2–5 cm.: herbage glabrous: stemless, or stems long (2–3 dm.), weak and procumbent and bearing several normal leaves: leaves mostly on the crowns of the caudex, crowded; the petioles very slender, 3–10 cm. long; the blade ovate, 2–5 cm. long, tapering rather gradually from near the base to the obtusish apex, the base roundish and shallowly cordate, the margin obscurely crenate and smooth; stipules greenish, linear, with few–many filiform pinnately arranged lobes or teeth: peduncles filiform, about

as long as the petioles, or if borne on the stems nearly as long as the whole of the subtending leaf: flowers (at least the late ones) rather small, blue: sepals lance-linear, less than half as long as the petals: lateral petals broadly spatulate, about 1 cm. long, a circular spot near one margin (toward the base) covered with rather long stiff white hairs; lower petals obovate, emarginate, 15–18 mm. long (including the straight spur with its abruptly bent acute tip): stigma obscurely pubescent: capsule smooth: seeds brown, with a pale conspicuous strophiole-like attachment.

There seems to be no near relative of this among the western species of *Viola*.

I have pleasure in dedicating this apparently strong species to Miss JUNE CLARK, of Boise, Idaho, who made an extensive collection of the plants, in duplicate, in her home neighborhood and in the mountains of Washington County, during the season of 1911. Her no. 84, from Clear Creek, in the Boise Mountains, July 4, 1911, is the type.

CHRYSOTHAMNUS OREOPHILUS **artus,** n. var.—Differing from the species in the stricter, narrowly racemose panicle, the filiform semi-cylindrical leaves, and the more glutinous involucres.

Secured by Miss CLARK, near Boise, September 1, 1911, no. 317. Collected also by HENDERSON at Nampa, July 30, 1897, and by CUSICK in Eastern Oregon, September 7, 1900, no. 2503. Distributed by them as an unnamed variety of *C. graveolens*.

CHRYSOTHAMNUS PUMILUS **latus,** n. var.—Distinguished from the species by the thin, flat, broad leaves (5–8 mm. wide) and the small cymose corymbs.

Were one to see just the herbage of this plant, it might readily be mistaken for some *Chrysopsis*.

NELSON and MACBRIDE'S no. 1236, Ketchum, Idaho, July 20, 1911, is typical. Certain numbers by other collectors seem to be more or less intermediate.

ERIGERON FILIFOLIUS **Bloomeri,** n. comb.—*E. Bloomeri* Gray, Proc. Am. Acad. **6**:540. 1865; *E. fissuricola* A. Nels. in Herb.—Perhaps no better example has been afforded of that form of error which comes from founding a species upon a single collection, or even upon several, when those represent a mere fraction of the range of the plant as it later comes to be known, than is supplied by what we now know of *E. filifolius* and its near allies. Whether this

liability of making a mistake, because of lack of knowledge of the variability and range of the plant in hand, is so grave a matter that one ought to be deterred altogether from founding a species upon a single collection may well be questioned. No doubt there are those who would take the affirmative, but general adherence to such a practice is manifestly impossible and probably also undesirable. To begin with, it would bar out the amateurs and amateurs are the stuff out of which professionals (experts) are made. It would defer publication of even the best of species, often indefinitely, and that is to kill interest and delay development. There would be little incentive to make collections were it understood that some one in the next generation would make report upon all except the well known things. That it is desirable to avoid the making of useless synonyms cannot be too strongly emphasized, but even a few synonyms is to be preferred to stagnation and death.

Nevertheless, such an array as the following ought to secure renewed caution in the best of us and deep penitence in the worst of us. Those who lament (and that includes the "chiefest sinners") are prone to think that great facility (perhaps agility) in making synonyms is peculiar to the present generation. Let us see how these examples (scores of others, just as illuminating might be found) bear out that idea.

DOUGLAS collected two plants in the region of the Columbia which were described in HOOKER'S *Flora* (**2**:20. 1834) as *Diplopappus filifolius* and *D. linearis*. The first of these NUTTALL transferred, and it became *Erigeron filifolius* (Trans. Am. Phil. Soc. **7**:328. 1841), although he probably did not himself know the plant, since the canescent paniculately branched stems and the yellow flowers mentioned by him do not belong together. In the meantime DECANDOLLE had based another name upon the same Douglasian collection, viz. *Chrysopsis canescens* (Prodr. **5**:328. 1836), and in spite of the fact that he speaks of the flowers as yellow, the chances are that this name refers to *Diplopappus linearis*, at least in part, just as NUTTALL'S name does. In the TORREY and GRAY *Flora* (**2**:177. 1842) this difficulty is not cleared up, but the true facts are suggested, in part, while they are also obscured by the retention of NUTTALL'S *E. ochroleucum* (*loc. cit.*), to which HOOKER'S

D. linearis is referred. Following this, apparently not much is gained by the publication of *E. pumilus* Hook. (Lond. Journ. Bot. **6**:242), nor the new combination (*E. canescens* Parry [Jones Exp.], no. 239), for GRAY refers both of these also to *E. ochroleucum*. GRAY in the *Synoptical Flora* (**1**:213. 1884) continues the confusion that had been increased by the publication of *E. peucephyllus* (Proc. Am. Acad. **16**:89. 1880), in which characters belonging in part to both of HOOKER'S species are combined.

These facts have been recited merely to show the impossibility of foreseeing the degree of variation or even the direction in which it will tend; hence the synonyms. Incidentally it shows that synonyms are inseparable from any period of great botanical activity, even when the work is in the hands of such veritable princes in systematic work as HOOKER, NUTTALL, TORREY, GRAY, and PARRY.

In 1865, GRAY published *E. Bloomeri* (Proc. Am. Acad. **6**: 540). Taking the material then available he was more than justified. It has taken nearly half a century of additional exploration to lead any one to question its validity. It happened that the first specimens of it represented it in its most depauperate stage, from the arid mountains of Nevada. Subsequent collections greatly extend its range, and a series of specimens leading straight into typical *E. filifolius* is now at hand, and may no doubt be duplicated in many of the larger herbaria. Even its raylessness is not an infallible character. MACBRIDE secured at Silver City, on a stony hilltop, a series of specimens that, if sorted and reported upon by one not familiar with their history, would appear as *E. Bloomeri* (rayless) and *E. filifolius* (radiate). These grew intermingled and were intentionally collected together and placed together upon the sheets to emphasize that fact. Under the circumstances one may even wonder why retain the name at all, but in view of the marked differences between the extremes in the series, perhaps the name had best stand varietally for the rayless forms.

In COULTER and NELSON'S *New Manual of Botany* (p. 527), the opinion is expressed that *E. curvifolius* Piper, Bull. Torr. Bot. Club **27**:396. 1900, is the same as *E. luteus* A. Nels., Bull. Torr. Bot. Club **27**:33. 1899. More careful scrutiny indicates that that opinion

was not well founded. The *Chrysopsis hirtella* DC. Prodr. 5:327. 1836, upon which PIPER's species was based, has a characteristic pubescence that separates it from *E. luteus* and *E. filifolius* as well. Since, however, there is nothing but its pubescence to separate it from the latter, it may as well become

ERIGERON FILIFOLIUS **curvifolius,** n. comb.

The status of *E. luteus* A. Nels (*loc. cit.*) cannot yet be passed upon with certainty. So far only the type collections are available, and these show some characteristics of habit and habitat that may denote its distinctness. If it is ever reduced it will be to separate varietal rank under *E. filifolius*.

ERIGERON COMPOSITUS **breviradiatus,** n. var.—Tufted on the crown of a solitary taproot, nearly glabrous: peduncles stouter and heads larger and broader than in the species: rays white to pale blue, broad, shorter than the disk flowers and barely surpassing the involucral bracts.

E. compositus Pursh already has more described varieties than it needs (see COULTER and NELSON, *New Manual*, p. 528), but the form here characterized is so unique that it needs to be catalogued in some way.

Secured by MACBRIDE at Silver City, June 17, 1911, no. 899.

Cordylanthus (ADENOSTEGIA) **bicolor,** n. sp.—Pilose throughout, with gland-tipped, subviscid hairs: stems mostly simple at base, rather freely branched upward, 3–5 dm. high: leaves 2–5 cm. long, linear and entire, or pinnately 3–5-divided; lateral lobes much shorter than the terminal, widely divaricate: heads terminating the branchlets, mostly 3 or 4-flowered, subtended by 4–6 foliar trifid bracts as along as or surpassing the flowers: calyx purple or purplish, diphyllous, the upper sepal 2-nerved, bifid, 10–12 mm. long; the lower oblong and entire, 3-nerved below, 5-nerved above, as long as or longer than the corolla: corolla purple, tipped with bright yellow, about 15 mm. long; the two lips equal, both appearing as if entire, but the lower with a rounded obtuse apex, the sides infolded and with an ovate tooth longer than the middle lobe; the sinuses plicate and having two thin lanceolate teeth: stamens 2; the anthers 1-celled, pubescent at both base and apex, the second cell represented by a pubescent rudiment, attached to the filament just below the fertile one; filament flattened and

with a U-shaped curve near the top: the stigma on the thickened inflexed tip of the style just protruding from the orifice of the folded galea-tip: capsule elliptic-oblong, few-ovuled, 4–6 maturing.

That this has passed for *C. capitatus* Nutt. seems quite probable. That it is in reality quite distinct the following differences indicate conclusively. No authentic specimens of *C. capitatus* are at hand, but it does not seem probable that NUTTALL, GRAY, WATSON, and others have all overlooked or that they would have been silent on the following points: the glandulosity; prevalence of pinnatifid leaves even below; the open panicle branching (not fasciculate-capitate); the bracts in excess of the flowers in the head; the unequal calyx leaves; the inflexed lateral lobes of the lower lip of the corolla; the laciniate plicae in its sinuses; the curved filaments and the rudimentary anther cell; and the beautiful purple of the flowers emphasized by the yellow, pubescent corolla tips.

Secured by NELSON and MACBRIDE on moist sagebrush slopes, at Ketchum, Blaine Co., July 20, 1911, no. 1239 (type); MACBRIDE, at Pinehurst, August 17, 1911, no. 1671.

Pentstemon brevis, n. sp.—Densely matted in tufts few–several dm. in diameter: roots woody, numerous, intricately interwoven: stems very numerous, borne on the crowns of the short slender subterranean branches of the caudex, usually 5–8 cm. high, though sometimes higher, very minutely puberulent as are also the leaves: leaves entire, moderately thick; the lower from oblong-elliptic to oblanceolate or spatulate, obtuse or subacute, 5–10 mm. long, tapering to a petiole often as long; stem leaves becoming sessile and narrower: inflorescence a narrow glandular-pubescent thyrse: calyx cleft into broadly lanceolate lobes 3 mm. or less long, rather thick and green except near the base: corolla dark-blue, slender, nearly tubular, 6–8 mm. long, bilabiate, with short rounded lobes and with short yellow pubescence in the throat and on the sterile filament: anthers dehiscent from the base and confluent but not explanate.

This species reminds one, in its low densely matted habit, of *P. caespitosus* Nutt., but in other respects it is more suggestive of a diminutive *P. humilis* Nutt. No one seeing these three species in the field, or even in dried specimens, will doubt their distinctness. *P. brevis* is alpine on wind swept summits.

NELSON and MACBRIDE, no. 1457, Lemhi Forest, Mackay, Custer County, Idaho, July 31, 1911. The only other specimen, seen by the writer, that approaches this species is CUSICK'S no. 1974, from bleak summits of Stein's

Mountains, E. Oregon, distributed as *P. humilis*, but which it is not. CUSICK'S specimen is larger in every way and less leafy on the stems.

Artemisia potens, n. sp.—Growing in small dense patches, the nearly simple virgate stems each from a long horizontal rootstock: stems rather slender, pale-green, slightly striate, minutely puberulent, 4–8 dm. high: leaves 3–6 cm. long, pale-green and glabrate above, thinly tomentose below, the margins revolute, simple or pinnatifid, the few (2–4) divaricate lobes and the body linear or nearly so: panicle narrow, dense, 7–15 cm. long: heads numerous, subspherical, 2–3 mm. high: involucral bracts oblong to oval, with greenish center, nearly glabrous, the delicately scarious margins appearing as if obscurely fringed: bracts linear, 1 or 2 to each cluster of 3–6 heads, longer than the heads they subtend and often nearly as long as the cluster: flowers 20 (more or fewer), the marginal ones pistillate, the inner perfect, all fertile: achenes glabrous.

In floral characters this is near *A. discolor* Dougl., but the aspect is that of *A. aromatica* A. Nels. or *A. redolens* Gray. In *A. potens* the heads form a long compact panicle and are as nearly erect as their crowded condition will permit. *A. discolor* has a woody caudex; *A. potens* is herbaceous to the ground. *A. discolor* grows in the moist rich soil of the mountains; *A. potens* on the dry saline-gravelly clays of the plains. The name refers to the overpowering but wholly characteristic *Artemisia* odor.

Type from Mackay, July 30, 1911, no. 1413, by NELSON and MACBRIDE.

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LARAMIE, WYOMING

TWO SPECIES OF BOWENIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 162

CHARLES J. CHAMBERLAIN

(WITH FOUR FIGURES)

All the cycads except *Bowenia* have pinnate leaves, so that bipinnate leaves make *Bowenia* a very unique genus. It is found only in Australia, and even there is limited to Queensland, ranging from the northern part of the state to about the latitude of Rockhampton, in the Tropic of Capricorn.

Bowenia is described as monotypic, with *B. spectabilis* as the only species, although taxonomists recognize a var. *serrata*, which is often called *serrulata*.

B. spectabilis is found in the northern part of the range. I found it at Babinda, near Cairns, and followed it for some distance toward Innesfail, where it was said to be fairly abundant. Mr. J. H. BAILEY, director of the Brisbane Botanical Garden, told me that it is abundant at Cooktown; others, not professional botanists, claimed to have seen it much farther north.

B. spectabilis var. *serrata*[1] is so abundant in the Maryvale and Byfield region near Rockhampton that it forms a dense, but easily penetrated underbrush in the prevailing *Eucalyptus* bush. Mr. R. SIMMONS, of Rockhampton, gave me directions for reaching this *Bowenia* locality. I studied the variety for a distance of 20 miles and did not see a single plant resembling the species. Similarly in the Babinda region I had not seen a single specimen which could have been mistaken for the variety. In fact, the differences between the two are so pronounced that they should be regarded as distinct species.

[1] **Bowenia serrulata** (André) Chamberlain, n. comb.—*B. spectabilis* Hook. f. var. *serrulata* André, Ill. Hort. **26:** 184. *pl. 366* (1879); *B. spectabilis* var. *serrata* Bailey, Queensland Flora 1507 (1902).—Caudex subterraneus sphaericus supra multicaulis; caulibus caespitosis 1–2 m. altis; foliolis serratis.—Vicinity of Rockhampton, Queensland.

Whether the margin of a leaflet is entire or serrate or spinulose may be trivial in some cases and important in others, even within the range of a single family. *Dioon spinulosum* was for a long time characterized almost solely by the spinulose leaflets, but the character is so constant that determinations based only upon this feature are quite safe. On the other hand, the leaflets of the African *Stangeria paradoxa* may show the entire or the serrate character on the same plant or even on the same leaf. In the Botanical

FIG. 1.—*Bowenia spectabilis* at Babinda, Australia: about 1 m. in height

Garden at Durban, South Africa, Mr. WYLIE showed me a plant of *Stangeria paradoxa* with leaflets so deeply incised that the leaves might almost be called bipinnate. In *Stangeria* the character is so fluctuating that it is of no taxonomic importance. In some species of *Encephalartos* the fluctuating variations in the margins of leaflets have doubtless led taxonomists into pitfalls.

In *Bowenia* the serrate or entire character of the margin is so constant that it would be worthy of specific rank even if it were not

correlated with the difference in geographical distribution and other features.

As found in nature, the species and the variety are noticeably different, the latter having a greater display of foliage (figs. 1 and 2). The species is most abundant in open places and clearings, while the variety is most abundant in the bush. Many specimens of the species in shaded places along streams are larger and taller than forms growing in the open, the leaves sometimes reaching a length

FIG. 2.—*Bowenia serrulata* at Byfield, Australia: about 1.3 m. in height

of nearly 2 m., while those in the open seldom exceed a meter in length, but the leaflets of plants growing in the shade never become spinulose. The leaves of the variety range from 1 to 2 m. in height, with about 1.3 m. as the prevailing size. The leaves are dark green, very glossy, and they retain their beauty for a long time, especially in the species, some leaves of which, after lying for three days on a veranda in the blazing tropical sun of Babinda, still looked almost as fresh as when taken from the plant. The sub-

terranean stem has a remarkably tenacious hold on life. Mr. EDWARD MEILLAND, who lives in the *Bowenia* region, told me that a stem just beneath the beaten path under the house had not produced a leaf for 20 years, but when the old house was abandoned and the path no longer used, the stem, so long dormant, produced a fine display of foliage.

The most striking difference between the species and the variety is in the stem, which is subterranean in both. In the species the stem is somewhat carrot-shaped, with one or two, sometimes four or five, slender branches at the top (fig. 3). These slender branches bear all the leaves and cones.

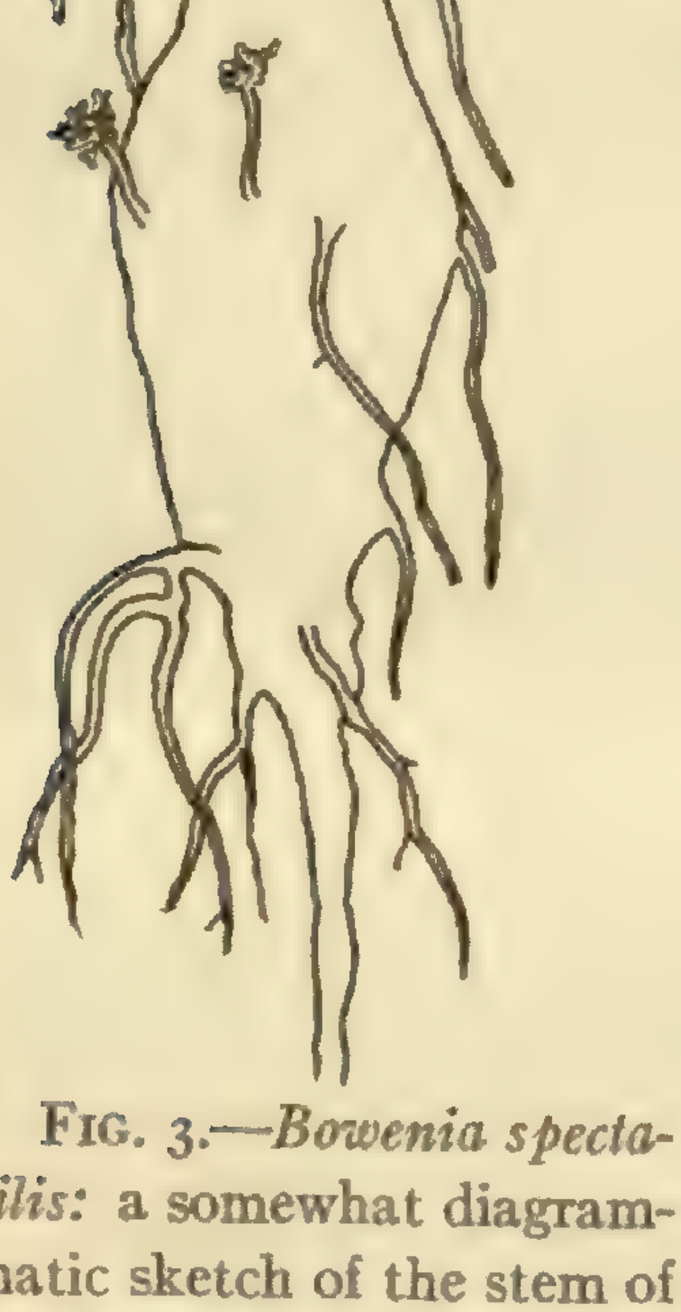

FIG. 3.—*Bowenia spectabilis:* a somewhat diagrammatic sketch of the stem of an ovulate plant; the portion shown is somewhat less than 1 m. in length; the dotted line is the ground line.

FIG. 4.—*Bowenia serrulata:* a somewhat diagrammatic sketch of the stem of a staminate plant; the stem is about 23 cm. in diameter; the dotted line is the ground line.

Sometimes they extend to the surface, but generally the bases of the leaves and the lower third of the cone are covered by the soil. Root tubercles are present but are generally 10–20 cm. below the surface.

In the variety the stem is spherical or turnip-shaped, usually about the size of a man's head, and has 5–20 slender branches at the top, like those of the species, only more numerous and reaching to the surface or even a little above (fig. 4). The slender branches themselves often branch. As a consequence, the foliage display is much greater in the variety than in the species. Usually, the slender branch bears only one leaf at a time, but two or three leaves are sometimes present. Cones are borne only on the slender branches.

In both species and variety the slender branches arise from buds at the top of the main stem, the buds often being due to injuries. Where the main stem has been torn by the plow, numerous buds may start.

Considering the difference in geographical distribution, the difference in leaflets, and particularly the striking difference in the stems, I have suggested that the variety be elevated to specific rank. I have had the assistance of my colleague, Professor J. M. GREENMAN, in the preparation of the description.

UNIVERSITY OF CHICAGO

BRIEFER ARTICLES

A NEW SPECIES OF ANDROPOGON

Andropogon urbanianus, n. sp.—Perennis; culmis glabris, 60–120 cm. altis; laminis teretibus, glabris; racemis binis, 2–4 cm. longis, vagina longioribus; rachi villoso; spicula sessili glabra, a basi villosa, 5 mm. longa, arista 2 cm. longa; pedicelli sterili villoso, 5 mm. longo, spicula pedicellata 3 mm. longa.

Perennial; culms glabrous, 60–120 cm. high, branched above, sheaths villous on the margin and toward the summit, or glabrate; ligule membranaceous, ciliate, 2 mm. long; blades terete, channeled above, glabrous, the two margins of the channel scabrous, villous above at base, 10–20 cm. long, about 1 mm. thick, tapering to a fine point; racemes 2 from each sheath, silky but not densely so, 2–4 cm. long, scattered along the upper part of the culms, usually of unequal length, the rachis joints slender, villous with long hairs, the subtending sheath shorter than the racemes; sessile spikelets 5 mm. long, glabrous, villous at base, scabrous above on nerves and keels, the awn geniculate, twisted below, 2 cm. long; sterile pedicel about as long as sessile spikelet, villous with hairs as much as 1 cm. long; pediceled spikelet reduced to a scale 3 mm. long.

Type specimen collected in Santo Domingo, Prov. Barahona near Las Salinas, by Padre MIGUEL FUERTES, no 1420, Sept. 1911. Other specimens referred to this species are: CAMACHE (St. Michel), Haiti, "in prato montano sicco"; W. BUCH no. 1074; FURCY, Buch 961.—A. S. HITCHCOCK, *Washington, D.C.*

EVAPORATION AND THE STRATIFICATION OF VEGETATION

(WITH ONE FIGURE)

During some investigations of the evaporating power of the air in various plant associations, data were obtained that show the amount of increase in the atmospheric humidity of the confined area of a ravine, and that tend to emphasize the contention of YAPP[1] that the varying

[1] YAPP, R. H., On stratification in the vegetation of a marsh, and its relations to evaporation and temperature. Ann. Botany **23**:275–320. 1909.

evaporation conditions at different levels in the same plant association may permit plants to grow in close proximity with one another, and yet, vegetating principally in different strata, to be subject to rather widely different growth conditions. Evidence supporting this view has also been furnished by DACHNOWSKI[2] and SHERFF[3] from observations extending over comparatively brief periods, all of these observers working in swamp or bog habitats.

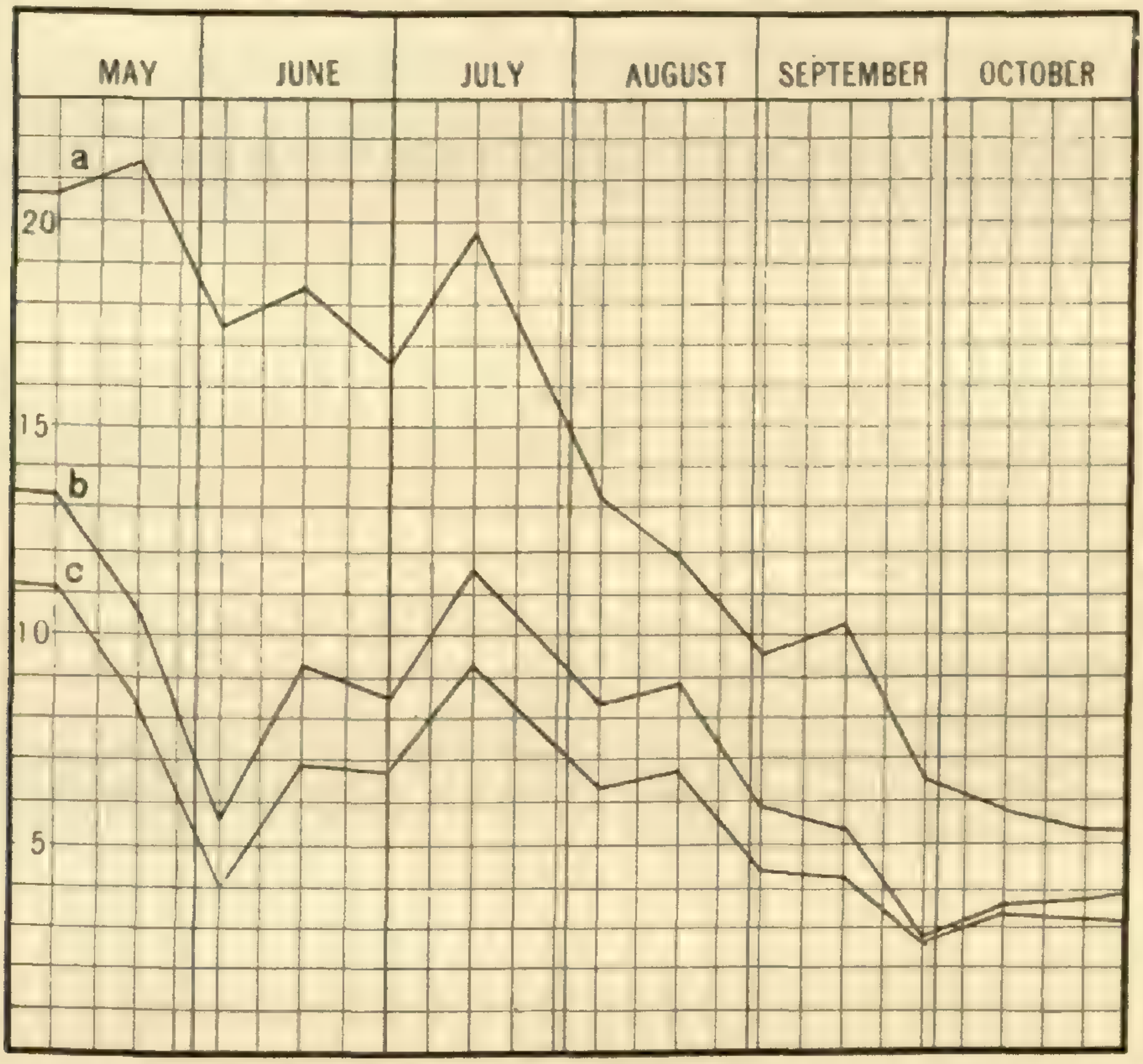

FIG. 1.—Diagram showing the average daily rate of evaporation in three strata of the beech-maple forest association for the growing season of 1911.

The present records were obtained during the season extending from May 1 to October 31, 1911, in some comparatively undisturbed beech-maple forests about 45 miles southeast of Chicago near the little village of Otis, Ind. The forest was of the usual climax mesophytic type. Its vegetation and the methods employed in obtaining the evaporation data by the use of the LIVINGSTON atmometers have been described in a

[2] DACHNOWSKI, A., Vegetation of Cranberry Island. BOT. GAZ. **52**:126–149. 1911.

[3] SHERFF, E. E., Vegetation of Skokie Marsh. BOT. GAZ. **53**:415–435. 1912.

previous paper.[4] The observations were made and the results have been plotted graphically for three different strata, with the intervals between the weekly readings as abscissae and the daily evaporation from the standard LIVINGSTON atmometer as ordinates (fig. 1). The intermediate graph (fig. 1*b*) represents the mean of three stations situated upon the forest floor, with the atmometers 25 cm. above the surface of the soil, in conditions of average vegetation. Here the average rate for the season was 7.4 cc. per day. The highest rate (fig. 1*a*) is that given by an instrument elevated 2 m. above the forest floor and shows an average of 13.5 cc. daily, or very nearly twice the amount of the stations immediately above the soil surface. The third record (fig. 1*c*) is for a station situated upon the slope of a ravine 10 m. deep, cut in the clay soil by a wet weather stream, and having a V-shaped outline in cross-section. The atmometer was placed 4 m. below the edge of the ravine and gave an average for the season of 5.9 cc. daily.

If the average rate of evaporation at the stations upon the forest floor be taken as unity, the proportional evaporating power of the air in the three strata will be found to be very nearly 1.84:1.00:0.80 for the season, and these figures may be taken to represent, more exactly than any previously available data, the measure of the mesophytism of these three several regions. It may also be noted that the elevated station has a much higher rate proportionally during the first half of the season.

The object of this paper being to indicate the amount of difference existing in the atmospheric conditions of some of the different strata of the same association, and to show how these differences may vary throughout the growing season, no attempt will be made to relate the vegetation to the different rates of evaporation. More extensive records must be obtained and an intensive study of the composition of the association undertaken before any satisfactory conclusions can be reached. It is interesting and important, however, to note the different atmospheric conditions to be encountered by forest tree seedlings during the first two years of their existence and at a later period when they reach the height of a meter or more. This may indicate one of the most important reasons why so many of the beech seedlings die before attaining the height of two meters. It may also be remarked that the lower evaporation in the ravine may be a sufficient explanation for the presence upon its slopes of a much greater abundance of such delicate forms as *Dicentra canadensis*, *D. Cucullaria*, *Impatiens biflora*, and *Asplenium angustifolium*.—GEORGE D. FULLER, *University of Chicago*.

[4] FULLER, G. D., Evaporation and plant succession. BOT. GAZ. **52**: 193–208. 1911.

CURRENT LITERATURE

MINOR NOTICES

Das Pflanzenreich.[1]—Part 46 is a monograph of the Menispermaceae by Professor LUDWIG DIELS. The author devotes about 45 pages to a general consideration of the family and then establishes 8 tribes which are based largely on the presence or absence of albumen and the character of the endocarp. These 8 tribes embrace 63 genera and 357 species; and approximately one-fifth of the total number of species are new to science. Two new genera are added, namely *Platytinospora*, based on *Tinospora Buchholzii* Engl. of tropical Africa, and *Sinomenium*, based on *Cocculus diversifolius* Miq. of Asiatic distribution.

Part 47 continues the monographic treatment of the Euphorbiaceae by Professor FERDINAND PAX, including only the tribe CLUYTIEAE. The author divides the tribe into four subtribes, namely CODIAEINAE, RICINODENDRINAE, CLUYTIINAE, and GALEARIINAE, depending on the number of stamens and the free or united petals. The tribe embraces 24 genera and about 150 species, 22 of which are new to science. One new monotypic genus (*Uranthera* Pax & Hoffm.) is proposed from the Malayan Peninsula. This part also includes an elaboration of the Cephalotaceae by Professor J. M. MACFARLANE. Only one monotypic genus of this family is known at the present time, namely *Cephalotus* from West Australia.

Part 48 continues the monographic treatment of the Araceae by Professor A. ENGLER, and contains the subfamily LASIOIDEAE to which are referred 18 genera and upward of 130 species, 18 of which are here published for the first time. One new genus (*Dracontioides*) is described, based on *Urospatha dehiscens* Schott of southern Brazil. *Amorphophallus* is by far the largest genus, being represented by about 75 species or more than one-half the total number recorded for the entire subfamily. Numerous and excellent illustrations amplify the text.

Part 49 contains a supplement to the Monimiaceae by Dr. JANET PERKINS, and records the results of a continued study of this family from new material represented in the leading European herbaria, particularly the Berlin herbarium

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[1] ENGLER, A., Das Pflanzenreich. Heft 46 (IV. 94). Menispermaceae von L. DIELS. pp. 345. *figs.* 93 (917). 1910. *M* 17.40. Heft 47 (IV. 147. iii). Euphorbiaceae-Cluytieae, unter Mitwirkung von KÄTHE HOFFMANN, von F. PAX. pp. 124. *figs.* 35 (144); (IV. 116). Cephalotaceae von J. M. MACFARLANE. pp. 15. *figs.* 4 (24). 1911. *M* 7.20. Heft 48 (IV. 23C). Araceae-Lasioideae, von A. ENGLER. pp. 130. *figs.* 44 (415). 1911. *M* 6.60. Heft 49 (IV. 101. Nachträge). Monimiaceae (Nachträge) von J. PERKINS. pp. 67. *figs.* 15 (112). 1911. *M* 3.60. Leipzig: Wilhelm Englemann.

through the rich collections of WEBERBAUER and ULE from South America and of MOSZKOWSKI, RÖMER, and SCHLECHTER from New Guinea and New Caledonia. Important data concerning older or little known species are recorded, and more than 30 species new to science are added to the monograph of this family by the same author, published in the *Pflanzenreich* in 1901. One new genus is proposed, namely *Carnegiea* from New Caledonia. All species enumerated are referred to in such a manner that the supplement can be used readily and advantageously with the *Monograph* itself.—J. M. GREENMAN.

The slime molds.—The second edition of LISTER'S *Mycetozoa*[2] is a notable contribution to our knowledge of these much discussed organisms. The new book follows the principal lines of the first edition, but has been improved and enlarged throughout. Six genera and 70 species have been added, so that the group now contains 49 genera with 246 species. The plates in the first edition were splendid, but those of the present volume are even better, and rank with the best illustrations which have ever been published of any plant structures.

Miss LISTER was constantly associated with her father in the preparation of the first volume, and the present work, published four years after his death, shows that she is able not only to make excellent illustrations, but also to organize and add to the text. It is distinctly a joint publication.

The "passing" of the slime molds is not referred to, the designation "organisms" being used in all cases, so that the title *Mycetozoa* is the only indication that the authors might be inclined to regard the organisms as animals rather than as plants. Until some decisive evidence appears, there is no reason for removing the specimens from the herbarium or for changing the library catalogues.—CHARLES J. CHAMBERLAIN.

Handbook of deciduous trees.—In 1904 SCHNEIDER'S *Handbuch* began to appear, and at the completion of the first volume (1906) it was reviewed in this journal.[3] Since that time the six parts constituting the second volume have appeared at intervals, and have been noted. Now the work has been completed with the appearance of the twelfth part and the general index.[4] As stated in preceding notices, it contains descriptions, with illustrations, of the angiospermous trees of central Europe, both native and under cultivation. The final part completes the dicotyledons (*Fraxinus* to *Metaplexis*), contains

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[2] LISTER, ARTHUR, and LISTER, GULIELMA, A monograph of the Mycetozoa, a descriptive catalogue of the species in the herbarium of the British Museum. 8vo. pp. 1–302. *pls. 201. figs. 56.* London: Printed by order of the Trustees of the British Museum. 1912.

[3] BOT. GAZ. **43**:43:214. 1907.

[4] SCHNEIDER, C. K., Illustriertes Handbuch der Laubholzkunde. Zwölfte Lieferung. Imp. 8vo. pp. 817–1070. *figs.* 515–628. Jena: Gustav Fischer. 1911. *M* 5. Also Register. pp. vii+138. *M* 5.

the monocotyledons (*Yucca* to *Agave*), and also an extensive supplement (pp. 869–1065) to all the preceding parts.—J. M. C.

North American flora.[5]—Volume **17,** part 2, contains the Poaceae (in part) from the genus *Arthraxon* to *Paspalum* by GEORGE VALENTINE NASH. One new genus is proposed, namely *Schaffnerella*, based on *Schaffnera gracilis* Benth. from Mexico. Several transfers are made, and new species are described in the following genera: *Schizachyrium* (4), *Andropogon* (1), *Amphilophis* (1), *Sorghastrum* (1), *Aegopogon* (2), and *Paspalum* (6).—J. M. GREENMAN.

NOTES FOR STUDENTS

Cytology of Polytrichum.—What is to be regarded as the first critical work on the cytology of mosses appears in a recent number of *Archiv für Zellforschung*. ALLEN[6] has studied and described with great care the structure and division of the antheridial cells of *Polytrichum*. For the sake of accuracy he finds it advisable to introduce several new terms: the cells which are to be metamorphosed into spermatozoids are referred to as *androcytes*, those of the penultimate generation as *androcyte mother cells*, and those of all the earlier generations as *androgones*.

In all androgones a deeply staining kinoplasmic mass is present in the cytoplasm; in the earlier generations it has the form of a large plate, while in the later generations it usually exists as a group of smaller bodies or "kinetosomes." All transitions between the two conditions are found. Previous to mitosis, the plate divides to two daughter plates, or in the case of the kinetosomes into two daughter groups, which move apart and occupy positions at opposite sides of the nucleus. Before the division of the plate a few achromatic fibers connect it with the nuclear membrane, and when the divergence of the daughter plates is complete these have increased greatly in number, determining the position and extent of the future broad-poled spindle. In the cells with kinetosomes there are no fibers discernible until the migrating groups reach their final positions. The spindle at length includes connecting fibers, mantle fibers, and usually a few short, freely ending ones.

The resting nucleus contains a single deeply staining mass made up of both nucleolar material and chromatin, and a sparse reticulum composed of chromatin and linin. As mitosis approaches, the nucleus enlarges until its membrane touches the polar plates or kinetosomes, while the material of the reticulum forms a spirem which segments into chromosomes. The presence of nucleoli at this stage offers additional evidence that the chromatin and nucleolar substance are distinct. The nucleus now collapses and the chromatin

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[5] North American flora, vol. **17,** part 2, pp. 99–196. New York Botanical Garden. September 18, 1912.

[6] ALLEN, C. E., Cell structure, growth, and division in the antheridium of *Polytrichum juniperinum* Willd. Archiv für Zellforschung **8**: 121–188. *pls. 6–9.* 1912.

becomes compacted into a tight knot. Soon the six chromosomes, all U-shaped and closely similar, disentangle themselves from this knot and become arranged on the spindle. They split longitudinally, separate, and reorganize the daughter nuclei in the usual way. During the anaphases and telophases the connecting fibers between the chromosome groups increase in number, pull away from the chromosomes, and become thickened at their ends. These thickenings apparently move toward each other and meet in the equatorial region, where by further swelling of the fibers the cell plate is formed. The splitting of the cell plate and the deposition of a wall between its halves were not observed, but are believed to occur.

In the androcyte mother cells there are a few granules, but nothing which can be certainly identified with the kinetosomes, whose bulk has been diminishing through the generations of androgones. There is, however, in each of them a small "central body" at the center of an aster in the cytoplasm. There is no evidence that it originates within the nucleus. It divides to two which diverge, each with an aster, to opposite sides of the nucleus. Some of the astral rays form cones whose bases are at the nuclear membrane, but between the separating daughter centers there is visible no constant connection. The central bodies are located at the sharp poles of the spindle, and as the nucleus swells it comes in contact with them. Although they are less conspicuous from this time on, it is reasonably certain that they persist in every instance through mitosis, which is essentially similar to that in the androgones. In the cytoplasm of each androcyte is a deeply staining granule occupying the position of the pole of the former spindle. This is the blepharoplast and is doubtless identical with the central body of the androcyte mother cell. The development of the spermatozoid is to be taken up in a later paper.

The spermatogenous cells are marked by a condition of polarity which persists throughout the life of each cell and is transmitted through a long series of cell generations. Except during mitosis, there is no trace of a polar arrangement of the nuclear structures.

The kinetosomes are believed to be not comparable to "chondriosomes" or other non-kinoplasmic inclusions of the cytoplasm. They are not definite morphological entities, but rather unorganized masses of reserve kinoplasm. The definite behavior of the plates in the early androgones is regarded as the result of the presence of a large amount of kinoplasm which tends to occupy a fairly definite position relative to the nucleus.

In contrast to the kinetosomes the blepharoplast is a definitely organized cell organ, and although the author believes that the question of its morphological nature is still an open one, he inclines toward the view that it is the homologue of a centrosome. This is strongly warranted by the centrosome-like behavior of the blepharoplasts in *Polytrichum*, with which he ventures to predict other bryophytes will be found to agree. The need of further researches among the Chlorophyceae for light on the origin of the blepharoplast is emphasized.

Although the mitosis in the antheridial cells of *Polytrichum* agrees in general with that in higher plants, certain peculiarities are pointed out which may prove to be of phylogenetic significance. Such are the delay in the preparation of the nucleus for division until after the formation of the spindle rudiment, the great swelling of the nucleus in one dimension during the prophases, the equatorial aggregation of the chromatin following the swelling, and the final shrinkage of the nucleus. It is yet too early to say whether any or all of these features are generally characteristic of mitosis in bryophytes, but many fragmentary observations make this appear quite possible.

The comprehensive review of cytological work in the bryophytes and the extensive list of literature brought together contribute much toward rendering this paper of the highest value to students of cytology.—LESTER W. SHARP.

Mallow rust.—In an elaborate paper ERIKSSON[7] gives the results of many years' investigations on the mallow rust, which, coming originally from South America, has been introduced into Europe, North America, and other countries. The work is replete with experiments and observations covering all phases of the biology and life history of this fungus, which presents peculiar features of interest, first, because in the countries into which it has been introduced it has spread to many plants not native in its original habitat, and second because, being one of the lepto-Uredinales whose teleutospores germinate at maturity, its manner of living from season to season has not been satisfactorily explained. It is in fact this latter phase of the subject which forms the pivot of ERIKSSON's investigation, and upon which he brings to bear the results of a vast amount of painstaking work.

The main contentions of ERIKSSON are that the fungus persists in the seed of infected plants in the form of a mycoplasma, and that it is disseminated chiefly by means of infected seed. The mass of experimental and observational data upon which he bases these contentions are briefly summarized here.

The historical data relating to the distribution of the fungus show that in many places it was first observed on plants grown from seed obtained from infected nurseries. The fungus is not spread to great distances by means of the sporidia. Wide dissemination is brought about by means of infected seeds or seedling plants containing the fungus in the mycoplasma stage. In plants grown from infected seeds the first outbreak of the disease occurs regularly when the plants are about three months old. This period is required for the mycoplasma to change into the filamentous stage and produce spore pustules. The pustules of the primary outbreak are very numerous and are uniformly scattered over the leaves of the young plant, while those of the

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[7] ERIKSSON, J., Der Malvenrost (*Puccinia Malvacearum* Mont.), seine Verbreitung, Natur, und Entwickelungsgeschichte. Kungl. Svensk. Vetensk. Handl. **47**: 5–120. *pls. 6. figs. 18.* 1911. For summaries previously published by the author see Compt. Rend. **152**:1776–1779. 1911, and Centralbl. Bakt. **31**:93–95. 1911.

secondary infection from sporidia are localized in groups near the points of infection. Neither the mycelium nor the spores survive the winter in Sweden. The teleutospores of this rust are of two kinds, and although they are morphologically indistinguishable, they behave differently on germination. Those of one type produce promycelia and sporidia in the usual way, but those of the second type produce slender germ tubes, whose terminal portions break up into several independent cells or conidia. The sporidia put forth germ tubes, which, penetrating the epidermis, make their way through the epidermal cells either directly into the intercellular spaces or into the palisade cells, and thence into the intercellular spaces. New sori result from these infections in 8–15 days. The conidia germinate, so to speak, by pouring their content into the epidermal cells, from which it migrates into the palisade cells, and finally through the entire plant. No outer visible sign results from these infections. The protoplasm of the fungus enters into a state of symbiosis with that of the host, thus forming the mycoplasm. The seeds of such infected plants produce seedlings in which the latent fungus manifests itself by a general outbreak of sori over the entire plant when it is about three months old. The change of the mycoplasm into mycelium is similar to that process described by the author in former papers.

Two other papers published shortly before the appearance of ERIKSSON'S account treat briefly of the mallow rust. In the first of these TAUBENHAUS[8] describes the two modes of germination of teleutospores noted by ERIKSSON, but, unlike ERIKSSON, he finds that the "conidia" abjointed by some of the germ tubes produce sporidia like other promycelial cells. Furthermore, he finds that the fungus is carried through the winter both by hibernating mycelium and by teleutospores. In plants in protected places, the mycelium resulting from late infections appears to produce sori, which develop slowly during the winter and mature the following spring. Regarding the hibernation of teleutospores, TAUBENHAUS finds that the teleutospores formed late in the season seem to behave like those of a *micro-Puccinia*. Some of these he found capable of germination during the winter and spring. With the advance of the season, however, the time required for germination increased from 24 hours to 6 days. This observation is quite contrary to the experience of DIETEL, who found that the period required for the germination of the teleutospores of *Melampsora Larici Caprearum*, a form with hibernating teleutospores, decreased with the advance of the season. Young seedlings may be infected by teleutospores borne in sori on the carpels and involucral bracts. Thus the fungus is distributed by means of infected seed and pieces of involucral bracts mixed with the seed, although the embryo is not infected.

In the second paper DANDENO[9] gives brief additions to his formerly

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[8] TAUBENHAUS, J. J., A contribution to our knowledge of the morphology and life history of *Puccinia Malvacearum* Mont. Phytopathology **1**:55–62. *pls. 3.* 1911.

[9] DANDENO, J. B., Further observations on the life history of *Puccinia Malvacearum.* Rep. Mich. Acad. Sci. **12**:91, 92. 1910.

published observations on the mallow rust. According to him the mycelium of the fungus lives through the winter in the stems and petioles of *Malva rotundifolia*, but the teleutospores do not survive the winter in Michigan.

Although ERIKSSON's observations have added many facts to those already known of the general biology of the mallow rust, his conclusion that the fungus lives through the winter only in the form of a mycoplasma in the seed or young plant is largely inferential, and one is inclined to give preference to the explanations of TAUBENHAUS and of DANDENO as less at variance with general experience than is the mystical mycoplasma.—H. HASSELBRING.

Germination.—The irregularity of the differences in rapidity and percentage of germination in the unlike seeds of heterocarpic plants under various conditions of germination, when the fruit and seed coats are left intact, is well shown in a lengthy paper by BECKER,[10] who studied in a rather superficial way the germination of 47 species of Compositae, several Cruciferae, and three Chenopodiaceae. Morphological position, the sexual condition of the flowers, darkness, temperature, increased and decreased oxygen pressure, nitric acid, and Knop's solution influence now disk seeds, now ray seeds, or both, or neither according to species, apparently without regularity. Age and possible sterility of the seeds are disturbing factors in the results. Most of the experiments were performed with fruit coats intact, but enough were removed to prove that the inclosing structures are largely responsible for these differences, which always become much less on removal of the fruit coat. These differences in germination do not, therefore, as ERNST and CORRENS assumed, rest on differences in the constitution of the embryos. This fact has been recognized here for some years, but has not been properly recognized abroad. Embryos of dimorphic seeds may and do differ, as the reviewer has shown[11] for *Xanthium;* but the differences due to embryos alone cannot be determined with seed coats left on the seeds. With *Axyris amaranthoides* BECKER does not get total failure of the round seeds to germinate, as did CROCKER[12] with seeds of this plant from our northwest, but merely a very low germination. This may be due to ecological differences in the regions where the plants grow affecting the seed coats.

As to the influence of increased oxygen, BECKER finds that brief exposure of seeds brings about the same kind of response as continuous exposure to high oxygen pressures, and argues therefrom that it exerts a chemical stimulus upon the protoplasm of the embryo, rather than increases the respiration as CROCKER has suggested. BECKER does not tell us what is the difference

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[10] BECKER, HANS, Über die Keimung verschiedener Früchte und Samen bei derselben Species. Inaug. Diss. pp. 7–129. 1912.

[11] SHULL, CHAS. A., The oxygen minimum and the germination of *Xanthium* seeds. BOT. GAZ. **52**:453–477. 1911.

[12] CROCKER, WM., Rôle of seed coats in delayed germination. BOT. GAZ. **42**:265–291. 1906.

between increase of respiration and his postulated stimulus. I have recently shown that there is a difference in the demand for oxygen by the embryos of the dimorphic seeds of *Xanthium*, and that the embryos do not germinate unless the minimum oxygen need is supplied. It cannot be doubted in the case of *Xanthium* that the oxygen is respired, and that up to the point where oxygen ceases to be a limiting factor, respiration increases with increased oxygen supply. If the seed coat structures limit oxygen sufficiently, the same conditions would obtain in any germination where free oxygen is necessary. BECKER'S contention, therefore, seems to be without sufficient foundation, especially since he made no attempt to measure the intensity of respiration under the conditions of his experiments. The idea that oxygen is a stimulus which "releases the mechanism" of germination is a conception typical of the German school of stimulus physiologists. BECKER is therefore orthodox in his interpretation of the less obvious chemical and physical changes in the germination of seeds. The Germans seem to find it difficult to grasp BLACKMAN'S conception of limiting factors, and apply it to the problems of plant physiology; or perhaps they merely prefer to leave the ultimate chemical phenomena of life and growth veiled under the term stimulus, which admirably conceals our ignorance of the real processes.

A study of the physical characters of the inclosing structures of the Compositae should disclose the causes of the irregular behavior BECKER reports, and careful exact studies of the chemical processes in the germinating seeds will show in how far the embryos are responsible for any of the noted differences.—CHARLES A. SHULL.

Cecidology.—Among the recent important European publications are the following: A paper by RÜBSAAMEN[13] on the cecidia of Africa and Asia describes and figures 38 cecidia from Africa and 6 from Asia. These are grouped with reference to the host plants and assigned to genera only. Most of the figures are for the purpose of showing the gross anatomical characters of the galls.

A paper by PANTANELLI[14] on the *Acarus* cecidia of the vine describes both the hypertrophies and the parasites. It is well illustrated with photographs of the injuries, microphotographs showing structures of the cecidia, and line drawings of the parasites. The subject is treated primarily from the standpoint of plant pathology and includes a description of one new species (*Phyllocontes viticolus*) and an excellent bibliography.

A paper by PARIS and TROTTER[15] gives a very important chemical study of the well known European gall of *Neuroterus baccarum* and the unaffected

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[13] RÜBSAAMEN, EW. H., Beiträge zur Kenntnis ausser-europäischer Zoocecidien. V. Gallen aus Africa und Asien. Marcellia **10**:100–132. 1911.

[14] PANTANELLI, E., L'Acariosi della vite. Marcellia **10**:133–150. 1911.

[15] PARIS, G., and TROTTER, A., Sui composti azotati nelle galle di *Neuroterus baccarum*. Marcellia **10**:150–159. 1911.

part of the foliage of the host plant. The analysis is interesting, but incomplete. The lengthy and well selected bibliography will be valuable for workers in biochemistry.

A paper by HOUARD[16] is subdivided into five parts as follows: (1) table of galls previously described, in which are listed 26 species with bibliography of each and grouped with reference to the host plants; (2) new observations upon the new galls of Tunis, in which the author gives brief discussions of 93 cecidia, some of which are assigned to genera only; these cecidia are also grouped with reference to the host plants; most of them are attributed to insects, one on *Moriandia cinerea* Cosson is caused by *Cystopus candidus*, one on *Olea europaea* L. is caused by *Bacillus olea* (Arc.) Trev., and a third is referred to as a fasciation without comment as to cause; (3) a very valuable bibliography on the zoocecidia of Tunis from 1894 to date; (4) a table of galls arranged with reference to host plants; (5) a table arranged with reference to the organisms causing the galls.

COSTERUS and SMITH[17] have represented a very interesting paper on tropical teratology. Malformations of 18 species (7 of which belong to the family Orchidaceae) are carefully described. These descriptions are far better than those frequently given in papers on teratology in that the relationships of the parts have been carefully worked out. No explanation is offered as to the cause of these peculiar structures.—MEL T. COOK.

Gas movements in plants.—It is a question of some interest whether static diffusion accounts for essentially all the gas exchanges of foliar intercellular systems or whether molar movement is also considerably involved. OHNO[18] has already shown how "hygro-diffusion" leads to such a molar extrusion of gas in the leaf of *Nelumbo nucifera*, and has explained the physics of the action. Now URSPRUNG[19] shows that the same process plays an important part in the gas movements in the leaves of *Nymphaea* and *Nuphar*. The first half of the article is devoted to a critical historical review of the work on *Nelumbo*. The conclusions reached agree with OHNO in all essential points, although that author has given the earlier literature a less critical consideration than is desirable. As URSPRUNG states, it has generally been believed that the observed gas exchanges and positive and negative pressures in the intercellular systems of *Nymphaea* and *Nuphar* are entirely determined by photosynthetic and respiratory activities. A mention of two of his experiments will show clearly that "hygro-diffusion" plays an important rôle in these forms.

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[16] HOUARD, C., Les Zoocédicies de la Tunisie. Marcellia **10**:160–184. 1912.

[17] COSTERUS, J. C., and SMITH, J. H., Studies in tropical teratology. Ann. Jard. Bot. Buitenzorg II. **9**:98–116. *pls. 5*. 1911.

[18] BOT. GAZ. **51**:310. 1911.

[19] URSPRUNG, A., Zur Kenntnis der Gasdiffusion in Pflanzen. Flora **104**:129–156. 1912.

If the cut end of a petiole of a leaf of *Nymphaea* is placed just beneath the water surface while the upper face of the leaf blade is in the air, gas of about the composition of the air continuously extrudes from the cut end of the petiole with pressures varying from 0 to 17 cm. of water, and in volumes amounting to several times that of the leaf in course of an hour. Both the pressure and rate of extrusion increase with a rise of the temperature of the leaf and with dryness of the air in contact with the upper surface of the blade, and ceases when the air over the blade is saturated or when the blade is immersed. By piercing the upper surface of the blade of *Nymphaea* just over the petiole repeatedly with a needle, turning up the margin of the blade, and supporting a little water over the punctures, a great extrusion of air can be demonstrated, increasing with the temperature of the leaf and with dryness of the air over the marginal region of the blade. This is almost identical with the main observations on *Nelumbo*, and is explained by the same physical principle. URSPRUNG believes that a considerable part of the gas exchange in leaves of water plants floating or borne above the water is brought about by "hygro-diffusion," but that it plays no considerable rôle in the gas exchange of land plants with their narrow intercellular systems, and of course no part in submerged leaves. The studies of OHNO and URSPRUNG now make possible a much more lucid statement of gas movements and pressures in the intercellular systems of plants than was formerly[20] the case.—WILLIAM CROCKER.

Cytology of rusts.—Investigations of the cytology of *Puccinia Falcariae* by DITTSCHLAG[21] and of *Endophyllum Sempervivi* by HOFFMANN[22] show that the sequence of nuclear phenomena in these forms agrees in its essential details with that of other rusts. Among the facts presented the following are of special interest. In *Puccinia Falcariae*, which is an autoecious form of the *Puccinopsis* type, the binucleate phase arises by the lateral fusion of the cells of a palisade-like layer differentiated near the lower middle of the young aecidium. Unlike the mode of origin of binucleate basal cells in the true aecidia of *Puccinia Poae* as described by BLACKMAN and FRASER, the mode of origin of these cells in *Puccinia Falcariae* resembles more nearly that usually observed in aecidia of the *Caeoma* type, in which the fertile cells are not overlaid with a mass of sterile tissue. Occasionally three cells fuse and thus trinucleate basal cells arise. Occasionally the basal cells branch and form more than one row of spores. Regarding the trichogyne-like cells observed by some investigators, the author states that the so-called sterile cells are not always present, but when they are they occur on both sexual cells.

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[20] PFEFFER, W., Plant physiology. Eng. ed. Vol. 1. pp. 199. 1899.

[21] DITTSCHLAG, E., Zur Kenntnis der Kernverhältnisse von *Puccinia Falcariae*. Centralbl. Bakt. II. **28:**473–492. *pls. 3. figs. 6.* 1910.

[22] HOFFMANN, H., Zur Entwicklungsgeschichte von *Endophyllum Sempervivi*. Centralbl. Bakt. **32:**137–158. *pls. 2. figs. 14.* 1911.

The life history of *Endophyllum Sempervivi* is peculiarly interesting because in that form the aecidiospores function as teleutospores. HOFFMANN finds that the binucleate basal cells arise from fusion of cells in the lower part of the aecidium. The axis of fusion, however, may lie in any direction, and there is no palisade-like arrangement of the fusion cells. The paired nuclei of the aecidiospore fuse and the subsequent processes are like those in teleutospores. The sporophyte phase is restricted to the aecidiospore mother cell and the two cells (aecidiospore and intermediate cell) formed from it.

In both of these forms the binucleate cells arise from the fusion of fertile cells, whose contiguous walls are dissolved. In this respect the process differs from the migration of nuclei through pores as described by BLACKMAN in his account of *Phragmidium violaceum*.

In a short note BEAUVERIE[23] reports further observations on the "corpuscules métachromatiques" which he finds in the mycelium of an unidentified rust of wheat and also in the host cells. The author now identifies these bodies with the "excretion bodies" of ZACH, and believes they remain in the host cells after the hyphae themselves have been digested.—H. HASSELBRING.

Embryo sac of Gunnera.—Ever since the investigation of *Gunnera* (Haloragidaceae) by SCHNEGG in 1902, the genus has been included with those interesting angiosperms (as *Peperomia*) displaying an excessive number of nuclei in the embryo sac preceding fertilization. It was very desirable to study the situation more critically, and this has been done by SAMUELS[24] for *G. macrophylla*. The sequence of events is as follows: The solitary hypodermal archesporial cell (mother cell) develops directly into the embryo sac, no tetrad in the ordinary sense being formed. At the first (heterotypic) division of its nucleus the reduced number of chromosomes was repeatedly observed to be 12. At the second division (four nuclei) two nuclei assume the micropylar polar position, and the other two are against the wall of the sac in the equatorial plane, and a little later move toward the antipodal pole. The polarity of the sac is thus attained at the 4-nucleate state. At this time the inner integument fuses to close the micropyle, and therefore the pollen tube was observed to pierce the integuments to reach the sac. The numerous vacuoles that appear during the second division fuse into a large central vacuole during the development of polarity. At the third division (eight nuclei) the upper one of the two micropylar nuclei divides to two nuclei side by side; and at the fourth division (16 nuclei) each of these two nuclei divides to two nuclei vertically placed. These four micropylar nuclei are the egg, the synergids, and the micropylar

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[23] BEAUVERIE, J., La signification des corpuscules métachromatiques dans les cellules de céréales infestées par la rouille. Compt. Rend. Soc. Biol. **70**: 461–463. 1911.

[24] SAMUELS, J. A., Études sur le développement du sac embryonnaire et sur la fécondation du *Gunnera macrophylla* Bl. Archiv für Zellforsch. **8**: 53–120. *pls. 3–5. figs. 23.* 1912.

polar, not merely in position but also in function. The micropylar polar then fuses with the upper six nuclei toward the antipodal region, resulting in a fusion nucleus of seven nuclei; while the remaining six nuclei form the antipodal complex. The cells of this complex enlarge after the entrance of the tube, but after fertilization they degenerate.

Spermatogenesis was also followed, verifying the chromosome count, and showing a remarkable behavior of the pollen grain in frequently sending two tubes into the same style. Double fertilization was observed, so that the endosperm-forming nucleus finally becomes a fusion of eight cells.

SAMUELS discusses at length the relation of such a 16-nucleate embryo sac to the embryo sacs of gymnosperms. He also concludes that such a sac represents four megaspores in its origin.—J. M. C.

Paleobotanical notes.—In 1906 SCOTT published briefly the genus *Botrychioxylon*, and now there has appeared the full account.[25] The genus is of special interest in being a true fern (Botryopterideae) in which a stele of simple form "has advanced in the direction of substituting secondary for primary xylem." There is also anatomical evidence that it holds an intermediate position between Botryopterideae and Ophioglossaceae, thus linking the latter with the ancient ferns.

ARBER[26] has described a new species of the problematical genus *Psygmophyllum*, from the Lower Carboniferous of Newfoundland, and in a revision of the genus recognizes six species, distributed from Upper Devonian to Permian. As to the affinities of the genus, nothing can be determined in the absence of fructifications. There is a suggestive resemblance of the leaves to those of *Ginkgo*, but ARBER is convinced that the similarity is purely artificial. He associates the genus with other genera of the Paleozoic (as *Ginkgophyllum*, *Dicranophyllum*, etc.) as a distinct group under the name *Palaeophyllales*, which may or may not have been the ancestors of the Ginkgoales.

Dr. STOPES[27] has recorded the existence of angiosperms in the Aptian (Lower Cretaceous) of England, an earlier horizon than any in which angiosperms were known to occur. The specimens are in the collections of the British Museum of Natural History, and have been made the basis of the description of three new genera (*Aptiana*, *Woburnia*, *Sabulia*). The structure of the wood lends no support to the view that angiosperms arose from gymnosperms, since it is like that of high-grade angiosperms in all details. The wood

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[25] SCOTT, D. H., On *Botrychioxylon paradoxum*, sp. nov., a paleozoic fern with secondary wood. Trans. Linn. Soc. London II. Bot. **7**:373–389. *pls. 37–41.* 1912.

[26] ARBER, E. A. NEWELL, On *Psygmophyllum majus*, sp. nov., from the Lower Carboniferous rocks of Newfoundland, together with a revision of the genus and remarks on its affinities. Trans. Linn. Soc. London II. Bot. **7**:391–407. *pls. 42–44. fig. 1.* 1912.

[27] STOPES, MARIE C., Petrifactions of the earliest European angiosperms. Phil. Trans. Roy. Soc. London B **203**:75–100. *pls. 6–8.* 1912.

does not occur in definite bundles, and the rays of *Aptiana* are multiseriate. The question of genetic connections must await further information, but the author well remarks that the chief importance of these three genera "is that they are so old, and that they prove the existence of undoubted higher woody angiosperms in Northern Europe at this time."—J. M. C.

The biology of Uredinales. An excellent summary of our knowledge of Uredinales is given by MAIRE.[28] Since the article is itself of the nature of a review, it needs to be mentioned here merely with reference to its scope, and to indicate new matter and views introduced by the author. The subject is treated under two heads: (1) the individual evolution and the sexuality of the Uredinales, and (2) the relation of the Uredinales to their hosts and to their environment.

The first part is chiefly an account of recent progress in the cytology of the rusts, with a brief exposition of the theories regarding their origin. The author himself believes the Uredinales and the higher Basidiomycetes to have had a common origin with the Ascomycetes. This view is based mainly on the presence of apparently functionless spermatia in the rusts and in some of the Ascomycetes, and on the existence of minute conidia possibly representing ancestral male cells among the Basidiomycetes.

In connection with the discussion of those rusts which have shortened life histories, the author introduces an amplification of SCHROETER's classification of these forms. By taking into consideration all the spore forms, including the spermatia, he obtains the following biological groups: O-I-II-III, *eu*-Uredinales; I-II-III, *cata*-Uredinales; O-II-III, *brachy*-Uredinales; O-III, *hypo*-Uredinales; O-I-III, *opsi*-Uredinales; I-III, *catopsi*-Uredinales; II-III, *hemi*-Uredinales; II, *pyro*-Uredinales. Heteroecism and autoecism are expressed by the prefixes *hetero-* and *auto-* in the manner suggested by DUGGAR.

The second part takes up such more general phases of the work on biology of rusts as the types of development of the Uredinales, the rôle of the different spore forms, dissemination and infection, and the more theoretical questions relating to the host-relationships and the origin of species and of heteroecism within the group, and finally the various types of morphogenic changes induced by rusts in their hosts.—H. HASSELBRING.

The mistletoes.—At the April meeting of the National Academy of Sciences, Dr. TRELEASE presented a revision of *Phoradendron*. An abstract of his paper is as follows: There are distinguished 83 forms of this exclusively American genus of mistletoes on the mainland north of the Isthmus, of which 72 are regarded as species and the remaining 11 as varieties. About half of them are Mexican, one-fourth Central American, and one-fourth belong to the

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[28] MAIRE, RENÉ, La biologie des Urédinales. Progressus Rei Bot. 4:110–162. 1911.

United States. Three main groups are recognized: one with very few-flowered spikes, growing on conifers, about equally divided between the United States and the Mexican highlands, comprising 12 species; one with more numerous flowers, growing on various angiosperms, comprising 11 United States and 18 Mexican species, also limited to the North; and one, differing from the second in the constant presence of scales at the base of at least its lowermost internodes, containing 14 Mexican and 17 Central American species. The first two groups are distinctly boreal and neither passes into the West Indies. The third group is distinctly equatorial, disappears well below the boundary between Mexico and the United States, and contains the exclusive representation of the genus in South America and the Antilles, more than half of its species occurring in this extralimital region. Except for two of these tropical species to which a wide range is ascribed, none occurs over so large an area as the common mistletoe of the eastern United States, which in distribution about coincides with the bald cypress.

A new aquatic fungus.—*Allomyces arbuscula*, a new generic type of the Leptomitaceae, has been described by BUTLER,[29] who found the fungus growing on dead flies in still water in Pusa and Poona, India. The individual plants consist of a basal cell which is attached to the fly by means of rhizoids, and at the apex branches more or less dichotomously to form a fan-shaped body of a few short cells. These give off slender branches which terminate either in zoosporangia or in sporangia containing a single thick-walled, brown resting spore. After the formation of a terminal sporangium, the axis is continued by a branch arising below the sporangium. Thus a sympodial system is built up as in *Phytophthora*. The fungus is peculiar in having a completely septate thallus, not usual among the Phycomycetes. The author regards it as a near ally to *Blastocladia* on account of the peculiar parthenogenetically developed oospores, which he suggests may have been derived from the *Monoblepharis* type through loss of the motile sperms.—H. HASSELBRING.

A bee hive fungus.—Miss BETTS[30] has described a new genus (*Pericystis alvei*) of "bee-hive fungus," which grows on pollen stored in the combs of the honey bee. The fungus is said to be "undoubtedly a normal inmate of the healthy bee-hive, and is, so far as is known, confined to that habitat."—J. M. C.

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[29] BUTLER, E. J., On *Allomyces*, a new aquatic fungus. Ann. Botany **25**: 1023–1035. *figs. 8.* 1911.

[30] BETTS, ANNIE D., A bee-hive fungus, *Pericystis alvei*, gen. et sp. nov. Ann. Botany **26**: 795–799. *pls. 75, 76.* 1912.

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THE
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THE LIFE HISTORY OF CUTLERIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 163

SHIGÉO YAMANOUCHI

(WITH FIFTEEN FIGURES AND PLATES XXVI TO XXXV)

Introduction

This paper deals with nuclear conditions in *Cutleria multifida* J. Ag. and *Aglaozonia reptans* Crouan, both of which are found in the Bay of Naples. In common with *Zanardinia*, another member of the Cutleriaceae, *Cutleria* and *Aglaozonia* are characterized by having large motile spores. The vegetative body and method of forming reproductive organs show a combination of characters found in *Ectocarpus*, *Sporochnus*, *Tilopteris*, *Sphacelaria*, *Battersia*, *Zonaria*, *Padina*, and *Laminaria*, genera belonging to different families.

The large motile spores attracted the attention of THURET (**63**), who was the first to do experimental work with *Cutleria multifida*. THURET was followed by many investigators who made cultures of the spores in order to determine whether *Cutleria* and *Aglaozonia* might be two alternating generations of one life cycle, but the results were conflicting.

FALKENBERG (**12**), working with material from Naples, first suggested that *Aglaozonia parvula* is the asexual form of *Cutleria multifida*, and that *Aglaozonia chilosa* is the asexual form of *Cutleria adspersa*. CHURCH (**6**), with material from Plymouth, connected *Aglaozonia reptans* with *Cutleria multifida*, and SAUVAGEAU (**43–51**), with material from Guéthary and Banyuls, proved that

Aglaozonia melanoidea is the asexual form of *Cutleria adspersa*. The conclusions of these authors were drawn chiefly from a comparison of young forms of *Cutleria* collected in nature with young plants obtained from cultures, the emphasis being laid upon outer morphological characters.

It is not necessary to present a detailed historical review of previous work, for many authors, especially SAUVAGEAU (**45**), have given such reviews. Since 1899 no work based upon original investigation has been published except by SAUVAGEAU and the present author. Papers by SAUVAGEAU (**46–51**) confirm his work of 1899, and a paper by the author (**76**) is the preliminary account of the present paper. Before turning to our own investigation, we shall indicate briefly what has been accomplished already, and what still remains to be done.

The first definite account of the discharge and the culture of spores of *Cutleria* was made by THURET (**63**), who observed that the female gametes germinated parthenogenetically. The male plants of *Cutleria* he found to be extremely rare at Saint Vaast-la-Hogue, France, where his cultures were made. This parthenogenetic product, a small plant somewhat resembling *Ectocarpus*, did not live long. According to SAUVAGEAU'S suggestions (**45**) the plant may be designated as form *Thuretiana*. Five years later the brothers CROUAN (**7**), by repeating these observations at Brest, France, came to the same conclusions. DERBÉS and SOLIER (**11**), working on the Mediterranean coast of France, confirmed THURET'S account. Thus these earlier observers, who worked on the French coast, seem to have entertained no doubt of the constancy of the parthenogenetic germination of the female gametes of *Cutleria*.

About two decades later two German botanists, REINKE and FALKENBERG, independently making cultures at the Naples Station, reported quite different results. REINKE (**38, 39**), working at the Station in 1875–1876, observed the actual fertilization of the female gametes by the male gametes of both *Zanardinia* and *Cutleria*. In vessels containing both male and female gametes germination took place freely. There seemed to be no germination of the unfertilized egg. REINKE concluded that sexual reproduction prevailed in *Cutleria multifida* and that THURET must have seen

only exceptional cases of parthenogenesis. He states that in the Bay of Naples the male and female plants occur in the ratio of 3 to 2. He obtained filaments of both *Zanardinia* and *Aglaozonia* which produced non-motile spores. In the cultures of *Cutleria*, *Desmotrichum* finally appeared, and consequently the ultimate products of the fertilized female gametes were not clearly followed.

FALKENBERG (**12**) in 1878, taking great care to obtain pure cultures of both fertilized and unfertilized female gametes, fully demonstrated the necessity of fertilization for germination. The female gametes, entirely separated from the male gametes, retained their capacity for fertilization for four or five days and then never grew beyond the formation of a thin cell membrane. FALKENBERG not only demonstrated the necessity for fertilization, but succeeded in developing the sporelings to a considerable size; in 6–8 weeks the sporeling in the stage of "foot embryo" (*Keimfuss*) had developed as a secondary lateral outgrowth the creeping flat form (*kriechende Flachsprosse*), which is identical with the creeping thallus of *Aglaozonia*. This kind of sporeling may be designated as form *Falkenbergiana*. FALKENBERG was the first to associate *Cutleria multifida* with *Aglaozonia reptans*, and *Cutleria adspersa* with *Aglaozonia chilosa*. Four years later JANCZEWSKI (**21**), at Antibes, did with *Cutleria adspersa* what REINKE and FALKENBERG had done with *Cutleria* at Naples, and showed that unfertilized gametes of *Cutleria adspersa* do not develop further.

In 1894 KUCKUCK (**24**) described a plant under the name of *C. multifida* var. *confervoides*. The plants came up in the tank of the Helgoland Laboratory in the summer of 1893, and were attached to stones which had been collected in the North Haven in fairly shallow water of 1–3 fathoms. The plants were monosiphonic and some of them were in the reproduction stage. The normal *Cutleria* is said to have been gathered at Helgoland by WOLLNY, but has not been known to occur there since. The origin of the plant is not clear.

The cultures of *Cutleria* and *Aglaozonia* made by CHURCH in 1898 were from material collected in English waters. CHURCH (**6**) obained the material by dredging in the estuary of the river Yealm, near Plymouth, England, at 2–3 fathoms below low water

mark. The male plants of *Cutleria multifida* were very rare, and in cultures of the female gametes there was produced parthenogenetically a form identical with the form *Falkenbergiana*. Further, from the zoospores of *Aglaozonia parvula* CHURCH obtained plants which, like the preceding, have the creeping platelike thallus of *Aglaozonia*, but whose column ends at the summit in filaments (not fascicled) which bear the male gametangia of *Cutleria*. The latter, being entirely a new form and having never been obtained by any previous investigators, may be designated as form *Churchiana*. Finding that the female gametes develop parthenogenetically and the zoospores of *Aglaozonia* produce *Aglaozonia* directly with no alternating appearance of *Cutleria*, CHURCH concludes that *Cutleria* and *Aglaozonia* represent simply polymorphism due to environmental conditions, especially such as changes in the temperature of water.

In 1898 SAUVAGEAU (**43**) reported that he found in nature, epiphytic upon adult *Cutleria adspersa*, a number of young sporelings of the same species. These sporelings were of two kinds, forms *Thuretiana* and *Falkenbergiana*, which were evidently growing side by side, at the same time, and on the same spot under similar conditions. In the summer of 1898, KUCKUCK (**25**) obtained in cultures at the Helgoland Laboratory a number of young plants germinating from the zoospores of *Aglaozonia parvula*. The young plants had the characters of the form *Thuretiana*, and in his material female gametangia of *Cutleria* were produced. Besides, some of the plants produced a creeping disk, so that the whole structure resembled the form *Churchiana*, but the form *Falkenbergiana* never appeared.

SAUVAGEAU (**44, 45**) found at several points on the coast of the Gulf of Gascony, France, a new *Aglaozonia*, the *Zonaria melanoidea* Schousboe, discovered at the beginning of the century at Maroc and not reported since, whose *Aglaozonia* nature remained unrecognized. SAUVAGEAU considers *Aglaozonia melanoidea* to be the sporophyte of *Cutleria adspersa*. In cultures of *Cutleria adspersa* which he collected at Guéthary (Basses-Pyrénées), he observed that the female gametes did not attract the male gametes. The female gametes germinated very readily parthenogenetically and

gave always and characteristically the form *Falkenbergiana*. In 1905 SAUVAGEAU (**47, 48**) collected *Aglaozonia melanoidea* at Banyuls-sur-Mer (Pyrénées-Orientales), and in winter and early spring in each successive year of 1905–1908, he (**46–51**) carried on his cultures at the Laboratory Arago, Banyuls. From the zoospores of *Aglaozonia melanoidea* he obtained, in a majority of cases, *Cutleria adspersa*, and in only one case out of 100 did he obtain *Aglaozonia melanoidea;* but neither the form *Churchiana* nor the form *Kuckuckiana* was produced. Unfertilized female gametes of *Cutleria adspersa* produced either *Aglaozonia* or *Cutleria*.

From his own results and those of previous investigations, SAUVAGEAU concluded that the alternation of two generations is not necessary, but rather, as it might be said, facultative. OLTMANNS (**35**), from results of previous authors, considers *Cutleria* as presenting no true alternation with the *Aglaozonia* generation, but as simply presenting another instance of polymorphism in algae. STRASBURGER (**59**), discussing the alternation of generations in Phaeophyceae, agrees with the views of SAUVAGEAU and OLTMANNS.

All these investigations, discussions, and conclusions were made without any reference to nuclear conditions. The cytology of *Cutleria* and *Aglaozonia* was first described by the author as a preliminary note three years ago (**74**).

The material for the present investigation was collected at the Bay of Naples in the winter of 1908 and spring of 1909, during which time I occupied a table of the Carnegie Institution at the Stazione Zoologica. *Cutleria multifida* was found growing on rocks at a depth of 1–5 meters in the vicinity of Posilipo and Castello dell 'Uovo, and *Aglaozonia reptans* was growing on the surface of echinoderm shells or stones in the same localities and also at Nisida along the Bay of Naples, often at a greater depth. A fresh and plentiful supply of material was furnished by Dr. SALVATORE LO BIANCO almost every day. Cultures of the plants and of their sporelings and the fixation of their critical stages were made in the laboratory of the Station, where by the kindness of Drs. ANTON DOHRN and REINHART DOHRN the author enjoyed every equipment for facilitating the work. The investigation thus begun at Naples was finished at the Hull Botanical Laboratory of the University of

Chicago. To Professor JOHN M. COULTER and Professor CHARLES J. CHAMBERLAIN I wish to express my thanks for their suggestions and criticisms throughout the investigation.

The paper presents the results of my studies on *Cutleria* and *Aglaozonia*. For *Cutleria* there is described the mitosis in the vegetative cells of the male and female plants, the formation of the male and female gametes, the fertilization and the germination of the fertilized female gametes, and the germination of the unfertilized female gametes; for *Aglaozonia* the mitosis in the vegetative cells, and the formation and germination of the zoospores. Finally, there is a brief discussion of the cytological phenomena and the alternation of generations.

Cutleria multifida

Cutleria multifida J. Ag. is generally dioecious, and the forms of the male and female plants vary with the localities in which they grow. At one place, the male plants are more broadly multifid and shorter than the female, which are very narrowly multifid and often reach a length of 25 cm. or more; in other localities the reverse is true, that is, the male plants are narrowly divided and larger than the female plants. An extensive comparative study of the forms shows that there is great variability in habit, so that it seems impossible to distinguish the two mature sexual individuals by any gross morphological aspects, except that they bear, as a rule, exclusively either male or female reproductive organs. *Cutleria* grows in the Bay of Naples upon rocks or mollusk shells, at a depth of 1–5 meters. The *Cutleria* material was collected with the rocks or shells upon which it was growing, and there was always an abundant display of the successive stages in the development of the plants, from the very young thallus to large adult forms. The young thallus is 1–3 mm. in length, narrowly funnel-shaped, and presents no feature to distinguish the male plants from the female.

MITOSIS IN THE VEGETATIVE CELLS OF THE MALE AND FEMALE PLANTS

Both male and female plants, when fresh, always bear a beautiful fascicle of hairs at the tips of the multifid filaments of the thallus, and scattered here and there upon the whole surface of the thallus

there are also tufts of hairs. Any part of the frond in vigorous growth is favorable for the study of vegetative mitosis, but details are more easily and definitely followed in the hairs and in the superficial layer of the thallus.

The cells in these regions are full of plastids, with usually a single nucleus in the center. The nucleus in the resting stage is very

FIG. 1.—*Cutleria multifida:* portion of a thallus with a number of filaments and young male gametangia.

small, generally about the size of the plastids or slightly larger (figs. 1, 5, 16, 53). The network is so fine that it is hard to recognize much chromatin in it. Neither centrosome nor central bodies with or without radiations seem to be present.

In early prophase the nucleus increases in size, until it becomes three or four times the diameter of the resting nucleus and is a conspicuous structure within the cell. During the growth of the

nucleus, just inside the membrane, there appear chromatin knots which are evidently worked out of the chromatin network by the rearrangement of the material. These chromatin knots, which are continuous with less deeply stained chromatin fibrils, are variable in number at first, but gradually the number of chromatin knots becomes definite and they are detached entirely from the chromatin fibrils and become the chromosomes, 24 in number (figs. 19, 54). The chromosomes, after segmentation, gradually assume a slightly elongated rod form and become arranged at the equatorial plate (figs. 20, 55).

A little before the equatorial plate stage, from the cytoplasm surrounding the nuclear membrane, kinoplasmic accumulations arise at the poles. A well marked centrosome-like structure in the kinoplasmic masses occurs only at the metaphase. The chromosomes split longitudinally and half of each chromosome proceeds to each pole (figs. 22, 56). During this entire process the spindle is intranuclear. At telophase the nuclear membrane disappears and the two sets of daughter chromosomes, crowded closely together, are surrounded by cytoplasm, and the formation of the nuclear membrane follows (figs. 28, 57).

When the daughter nuclei are organized, the central spindle disappears completely (figs. 29, 57). The cytoplasm lying between the two nuclei begins gradually to assume a coarse, irregular, alveolar structure, and the walls of the alveoli, probably after a change in their material, form a new cell plate. Vegetative mitosis is essentially the same in both male and female plants.

The size of the nucleus varies according to the portion of the thallus in which the nucleus is contained. The hairs and superficial cells contain larger nuclei than the huge cells situated below the superficial cells; however, even those in the hairs and superficial cells vary in size. There seems to be no relation between the size of the nucleus and that of the cell. Quite frequently the narrow cells in the hairs contain larger nuclei than the elongated cells; usually the marginal cells in the superficial layer of the thallus have larger nuclei than the others. On the whole, the nuclei of the female plants are slightly larger than those of the male plants. However, such a difference, if it exists, is not very great during the vegetative

division, but the conspicuous difference in size appears in the formation of the reproductive organs.

THE MALE GAMETANGIUM

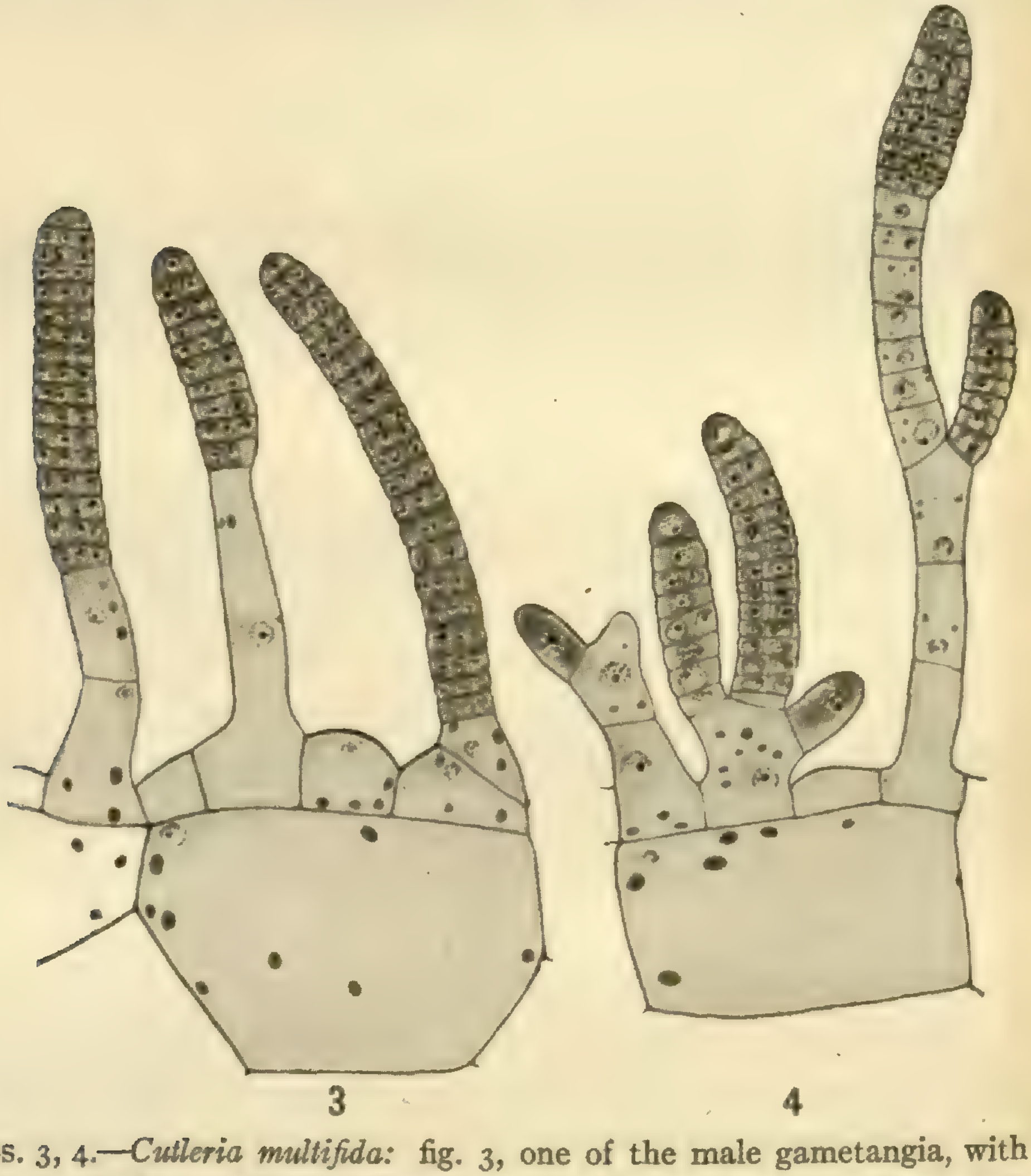
Mature male gametangia.—Male gametangia occur all over the surface of the thallus in small or in large clusters (figs. 1, 2, 3, 4). When the male plant is young, before the appearance of gametangia, the surface of the thallus bears tufts of hairs here and there in somewhat regularly scattered spots. Later, with or without the association of the hairs, young male gametangia appear. Both the male gametangia and hairs arise from superficial cells of the thallus.

The mature male gametangium consists of a number of tiers of small cells (the male gamete mother cells), each tier composed of 8 cells, and since there are more than 22 tiers (fig. 4), the output of male gametes from a single gametangium is about 200. The mature male gamete in the free swimming condition outside of the gametangium has an oval shape (fig. 8, *a*) and usually contains two plastids. Associated with one of the plastids, inside of the lateral face of the plasma membrane near the anterior end, is a red pigment, and in close association with this pigment are two cilia of different lengths, the long cilium directed toward the anterior end, 4.5 times the long diameter of the gamete, and the short one in the opposite direction, about twice the diameter of the gamete. The long diameter of the entire male gamete is 5 μ (figs. 3 and 4).

FIG. 2.—*Cutleria multifida:* a filament bearing a few male gametangia in successive stages of development.

Development of male gametangia.—As was stated above, both the hairs and gametangia arise from the superficial cells of the thallus.

One of the superficial cells commences to grow more vigorously than the rest (fig. 17) and a typical nuclear division takes place, which gives rise to a gametangium initial and a stalk cell. Some-



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FIGS. 3, 4.—*Cutleria multifida:* fig. 3, one of the male gametangia, with a long stalk composed of several cells; fig. 4, gametangia near maturity; one of them has 22 tiers of mother cells.

times 2–7 or more subsequent divisions occur and there is produced a filament of two or more cells, the terminal one of which is destined to be a male gametangium initial (figs. 1, 3, 4). Or a filament becomes a long multicellular structure of a single row of cells, and from a number of these cells there are produced lateral branches, consisting of one, two, three, or more cells, the terminal one of which becomes the gametangium initial (figs. 2, 21, 39).

The nucleus of the male gametangium initial is considerably larger than is common in cases of vegetative mitosis (fig. 18). The chromatin network of the resting nucleus is marked by a number of knots mixed with broken fibrils (fig. 18). The chromatin knots increase gradually in size in prophase and finally break up into 24 chromosomes (fig. 19). Up to this stage the nucleolus remains without apparent change. When the chromosomes begin to be arranged at the equatorial plate, the nuclear membrane becomes contracted, and at the completion of the nuclear figure the decrease of the diameter of the nucleus is remarkable (fig. 20). Two distinct centrosome-like structures now are present at metaphase. While the nuclear membrane still persists, the chromosomes split longitudinally and half of each chromosome proceeds to each pole (fig. 22). The nucleus passes into telophase, two new daughter nuclei are formed, and then the subsequent divisions occur. In the second division the two nuclei may undergo mitotic changes simultaneously, both showing 24 chromosomes in prophase (fig. 23), or one may proceed more rapidly than the other. Figs. 24 and 25 show the latter case; the nucleus of the upper cell is in prophase, showing 24 chromosomes, and that of the lower cell is in metaphase. In figs. 24 and 25, in spite of the apparent similarity in the size of the lower cells, the difference in the size of their nuclei at metaphase is remarkable. Sometimes the nucleus of the upper cell is far behind that of the lower cell in dividing, so that, as in fig. 26, the upper nucleus is in the resting condition while the lower one is in anaphase. Fig. 27 shows the nucleus of the upper cell in metaphase, which passes to anaphase (fig. 28) and to telophase (fig. 29) while that of the lower cell remains resting. When the filament has reached the 3-celled stage mitosis in the three nuclei proceeds in varying order. In fig. 30 is shown the case in which the nucleus of the basal cell is more advanced, revealing 24 chromosomes in prophase. The following figure shows the nucleus of the terminal cell in advance and now in metaphase. In the next figure the nucleus of the middle cell is already in anaphase.

At the 4-celled stage of the young gametangium, the nucleus in prophase invariably shows 24 chromosomes (figs. 33, 34). At about this stage the nucleus in division has almost the same size and

aspect as the nuclei in vegetative filaments. In figs. 35 and 36 are given anaphase and prophase of the vegetative division. Until about the 4 or 5-celled stage the young gametangium consists of a single row of cells, after which division also occurs perpendicular (figs. 37, 48) to the direction of the axis of the gametangium, so that there are two rows of cells. When the young gametangium has reached the 8 or more-celled stage and consists of two rows of cells, the nucleus in both the resting and dividing condition has necessarily been forced to assume a somewhat irregular form so as to occupy the largest possible space, and it does not decrease much in size in spite of the multiplied divisions and consequent diminution of the cells of the gametangium (figs. 40, 41).

Another division perpendicular to the direction of the growth of the gametangium occurs (figs. 42, 44), and the gametangium becomes a structure composed of four rows of cells. The diminution in the size of the nucleus is now recognizable (figs. 43, 45). Although the chromosomes which appear in prophase are 24 in number, their size has become remarkably reduced to about half the diameter of those appearing in earlier mitoses. The diminution may proceed still further during the divisions which multiply the number of the cells in a tier. There now occurs the third and last division perpendicular to the axis of growth of the gametangium (fig. 50), resulting in a structure composed of eight rows of cells. Even after the gametangium shows eight rows of cells, a number of mitoses may occur that increase the number of cells in the rows (figs. 46, 47, 48, 49), and during these mitoses there are always 24 chromosomes. These longitudinal divisions of the gametangium, as well as the transverse, are strictly simultaneous, but they proceed at a nearly uniform rate, so that ultimately there is formed the well known male gametangium of *Cutleria*, which is composed of eight rows of cells, each row made up of a varying number of cells. The number of cells in a row may be even more than 24, the cells of each row lying side by side with the cells of the contiguous row. Each individual cell in the gametangium is a male gamete mother cell, within which a single male gamete is formed.

The mother cell contains a single large nucleus situated in the

center, and usually two plastids whose position varies. The nucleus passes into a completely resting condition. Fig. 52 represents a cross-section of a male gametangium, each gamete mother cell showing a red pigment spot in close association with the nucleus. When the male gametes are mature within, a portion of the free surface of the membrane of the mother cell dissolves so as to leave a small pore, through which the gametes are discharged. The cilia of the gametes first protrude from the pore, keep moving for a while, and then all the contents emerge and the male gamete is set free.

FIG. 5.—*Cutleria multifida:* portion of a thallus with a number of filaments bearing female gametangia in various stages of development.

THE FEMALE GAMETANGIUM

Mature female gametangia.—Female gametangia are scattered over the whole surface of the thallus, as in the case of the male gametangia (figs. 5, 6, 7). The female gametangia are developed alone or are associated with hairs which appear upon the surface of the thallus long before the appearance of the gametangia. As in the case of the male plants, the hair and gametangium originate from superficial cells of the thallus.

The mature female gametangium consists of several tiers of female gamete mother cells, the number of tiers varying from 4 to 7. Each tier is composed of 4 or 8 mother cells, so that the output of gametes from a single female gametangium fluctuates between 16 and 56. The mature female gamete in the free swimming condition outside of the gametangium is oval (fig. 8, *b*), and usually contains more than 30 plastids. The anterior end of the body of the female gamete is destitute of plastids and contains colorless granular

cytoplasm, thus indicating the existence of polarity in the distribution of plastids. In association with one of the plastids, which is situated near the periphery in the vicinity of the anterior end, there is present a red pigment spot. Close to the pigment spot, two cilia of unequal length are borne; the long one being directed toward the anterior end, 1.5 times the long diameter of the gamete, and the short one in the opposite direction about equal in length to the

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FIGS. 6, 7.—*Cutleria multifida:* fig. 6, a filament bearing two female gametangia; fig. 7, female gametangia near maturity; *a* consists of 7 tiers of mother cells, and *b* of 4 tiers.

diameter of the gamete. The long axis of the female gamete is 26.2 μ. The female gamete is actively motile when discharged, but after a while the movement becomes sluggish, the shape becomes spherical (fig. 8, *c*), and the cilia are withdrawn.

Development of female gametangia.—Like the male gametangium, the female gametangium arises from a superficial cell of the thallus. One of the superficial cells begins to grow more rapidly than the others (fig. 53) and a typical mitosis takes place, which gives rise

to a gametangium initial and a stalk cell. Sometimes a second or third division is intercalated between the first division occurring in the superficial cell and the formation of the gametangium initial, and in this case the female gametangium, instead of having a stalk of a single cell, has a stalk consisting of two (fig. 7, *a*) or three cells (fig. 7, *b*). Or a number of divisions follow the first, so that the superficial cell develops into a long filament and some cell of the filament divides laterally to form a branch which becomes a gametangium initial (fig. 6).

The nucleus of the gametangium initial increases greatly in size, as in the case of the male gametangium initial. In it there is contained a large number of plastids. The chromatin network of the nucleus, which is composed of irregular knots and scanty fibrils during the resting stage, gradually increases in chromatin content, and finally there is established a prophase (fig. 54) containing 24 chromosomes and a single nucleolus. In metaphase the volume of the nucleus diminishes considerably (fig. 55), when compared with the previous stage, and centrosome-like structures appear at the poles. While the nuclear figure is still intranuclear, the chromosomes split longitudinally and half of each chromosome passes to each pole (fig. 56). At telophase two daughter nuclei are formed, and no central spindle remains between them. The cell plate is laid down by the cooperation of the vacuoles and rearrangement of the cytoplasm (fig. 57). Each nucleus of the two cells grows in size simultaneously during the resting condition (fig. 58) and then the rates of the mitotic processes in these two nuclei diverge; the upper nucleus enters prophase, showing 24 chromosomes (fig. 59),

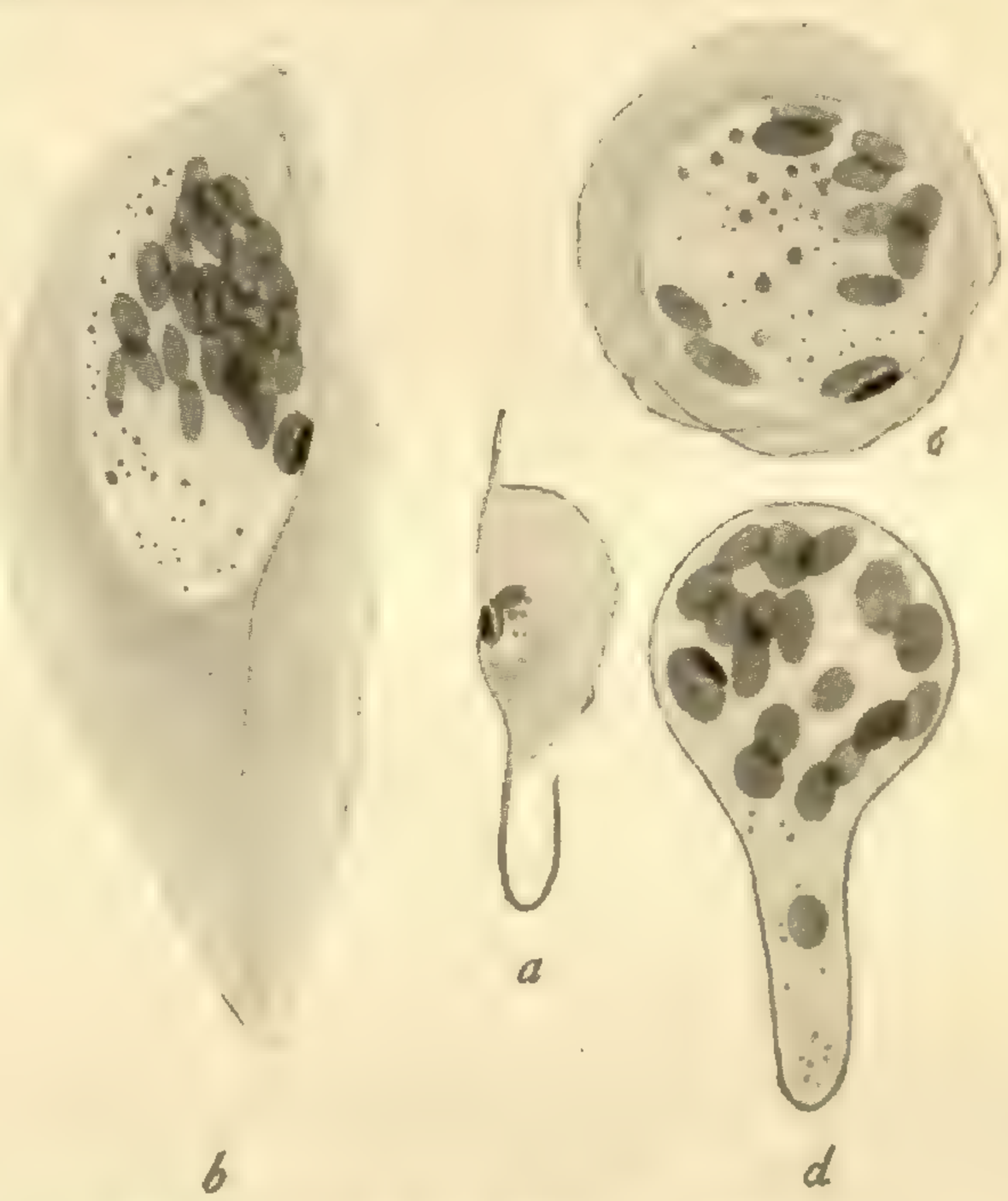

FIG. 8.—*Cutleria multifida:* gametes sketched from living material; *a*, male gamete; *b*, female gamete; *c*, female gamete which has become quiescent and spherical; *d*, female gamete germinating apogamously.

metaphase with two centrosome-like structures (fig. 60), anaphase (fig. 61), and reaches telophase (fig. 62) while the lower nucleus still remains in the resting condition. Sometimes the lower nucleus divides first, showing metaphase with two centrosome-like structures (fig. 63) and anaphase (fig. 64) while the upper nucleus rests.

In the young female gametangium, consisting of three cells, the mitoses occur in varying order; sometimes the nucleus of the basal cell divides first (figs. 65, 66), sometimes that of the upper cell (figs. 67, 68), and sometimes that of the middle cell (figs. 69, 70), and during these divisions 24 chromosomes are always seen in prophases (figs. 65, 66, 69, 71).

Up to the 4-celled stage the female gametangium divides transversely, and then a perpendicular division occurs (fig. 72), so that the gametangium consists of two rows of cells, after which another longitudinal division (figs. 73, 78) immediately follows and results in producing a gametangium of four rows of cells.

Mitosis in the gametangium of the 7–11-celled stage is not simultaneous, but occurs at different times in different cells. The nucleus in the middle cell may divide ahead of the others (figs. 74–77, 79, 80, 83, 84), whose nuclei are either in the resting stage or in prophase. The nucleus in prophase in any of these cells always presents 24 chromosomes, and in metaphase two centrosome-like structures are seen at the poles. It is remarkable that the chromatin knots or globules in the resting nucleus always lie quite independent of one another, the chromatin fibrils being so scanty that they are unable to connect them together.

In the young gametangia of the 10–18-celled stage, the mitoses take place as in earlier stages (figs. 85–88); the prophase and the polar view of metaphase show clearly that the number of chromosomes is 24. One striking feature as contrasted with the male gametangia is that in the female gametangia the nuclear diminution in size is not very great during the repeated divisions and consequent multiplication of cells of the gametangia. Of course the nucleus at the time of the first division in the female gametangium is rather large, especially in prophase (fig. 54), and the nucleus in the prophase of the division in the female gametangium of the 18-

celled stage is almost two-thirds of that diameter (fig. 87), but if the nuclei in metaphase and in the resting condition are taken into consideration, almost all of the cases in the gametangia from the 2-celled stage to 18-celled stage seem alike. The female gametangium, consisting of four rows of cells, becomes mature (fig. 89), but quite often each of the cells in the four rows divides again, so that the gametangium consists of eight rows of cells (fig. 90).

These numerous nuclear divisions are not simultaneous, but follow in regular order, both those which are transverse to the axis of the gametangium and those which are perpendicular to it, so that the ultimate result is the well known female gametangium of *Cutleria*, which is composed of four or eight rows of cells, each row composed of 4–7 cells, the cells of each row lying almost exactly opposite the cells of the neighboring row. Each individual cell of the gametangium is a female gamete mother cell. The mother cell contains a large nucleus either in the center or near the inner wall (figs. 90, 92). Plastids are crowded either near the inner wall (fig. 91) or near the outer side (fig. 92), or lie scattered regularly throughout the whole cytoplasm. The nucleus is in the resting condition.

When the gametangium is mature, the whole contents of a gamete mother cell become a single female gamete. A portion of the free surface of the mother cell dissolves and forms a pore through which the gamete is discharged. The slow process of discharging the gametes is the same as in the case of the male gametes; first, the cilia of the gametes appear outside the pore, keep waving for a while, and then the female gamete is set free.

FERTILIZATION AND THE GERMINATION OF THE FERTILIZED FEMALE GAMETES

The discharge of both male and female gametes occurs at almost any time during the day and night. However, so far as the writer's experience goes, while he was making observations at half hour intervals under the microscope, the majority of cases showed that the discharge was most abundant at 5 A.M., and that it continues, though gradually diminishing, until 7 A.M. and then ceases. Occasionally there is some discharge at 11 A.M. and 5 P.M. The motile

power of the male gametes continues for almost 20 hours, while that of the female gametes is comparatively short, the longest period of the swimming condition observed having been 2 hours, and the shortest 5 minutes. Toward the end of the motile condition in both male and female gametes, the movements become sluggish, and then cilia are no longer recognizable, seemingly being withdrawn or coalescing with part of the plasma membrane of the gamete body, and finally the shape of the body becomes spherical. However, in a number of cases gametes caught in the thallus of algae while swimming between the slide and cover-glass remained active for more than 24 hours, and then became spherical; when stained at that time they showed the cilia still persisting and not coalescent with the plasma membrane.

The union of male and female gametes and the subsequent nuclear behavior were studied in material from artificial cultures. A number of dishes were prepared containing either male or female plants bearing mature gametangia. When the discharge of gametes became abundant, the sea water of the dish containing thousands of swarming male gametes was added to a dish containing vigorous female gametes. Then part of this mixture was observed under the microscope in living condition and part was fixed every 30 minutes for 24 hours, and then at 26, 28, 32, and 48 hours, and later, every 3 or 5 days up to 75 days. The following description is based upon material obtained in this way.

The male gametes while swimming freely become attached to the female gametes which are either sluggishly swimming or have come to rest, but have not yet formed a cell wall. When the male gamete becomes quiescent, before coming in contact with the female gamete it withdraws its cilia and its shape becomes spherical. The nucleus is full of chromatin which is clearly broken into 24 independent chromosomes. The nuclear membrane is very delicate (fig. 94). When a male gamete has just become attached to the female gamete, both gametes have very delicate plasma membranes. The nucleus of the female gamete is at the center of the cell, as in the resting condition (fig. 95).

Then the plasma membranes which lie between the cytoplasm of the male and female gametes become obscure and the cytoplasm

of the two gametes comes into direct contact. The male gamete can be observed for a short time as a protuberance at the periphery of the female gamete (fig. 95); however, sooner or later the protuberance is entirely absorbed or leveled down to the surface of the now spherical female gamete. The male nucleus with 24 distinct chromosomes proceeds toward the resting female nucleus (fig. 96); it then proceeds still further (fig. 97) until it is close to the female nucleus (figs. 98, 99). The male nucleus at this stage is surrounded by a clear zone, which possibly means that the nucleus is carrying with it a part of the male cytoplasm or a part of the female cytoplasm which had been lying in the path of the male nucleus. The male nucleus now becomes closely applied to the female nucleus (fig. 100). The chromatin of the male nucleus becomes closely aggregated (fig. 101), and then begins to be finely alveolated (fig. 102), and finally becomes dispersed through the female nucleus as irregular knots (fig. 103). Later the fusion nucleus contains chromatin knots of various sizes and shapes, together with delicate, irregular, discontinuous fibrils. A nucleolus which was present in the female nucleus before the union still persists (fig. 104). The fusion nucleus thus passes into a completely resting condition, in which chromatin of male and female origin cannot be distinguished from each other.

Returning to the previous stage, at the time of the union both gametes are surrounded by plasma membranes only. At the time of the entrance of the male nucleus into the female cytoplasm the outermost layer of the plasma membrane is observed to change into cell wall (fig. 96), which is very thin at first, but gradually increases in thickness as fusion progresses, and is well organized by the time the fusion nucleus reaches the resting condition.

The first segmentation division of the sporelings of the fertilized gametes takes place 20–24 hours after the union of the gametes. In prophase there appear 48 chromosomes, all of which seem alike both in size and shape (fig. 106), and a single nucleolus persists. At metaphase the chromosomes are arranged at the equatorial plate and two centrosome-like structures appear at the poles (fig. 107). A comparison of the prophase and metaphase shows that the volume of the nucleus is considerably diminished at the

latter stage. The mitosis may take place before the sporeling begins to elongate; but in the majority of cases the sporeling elongates into a somewhat pear-shaped structure while its nucleus is still in the resting state (fig. 108). Quite often the nucleus is present at the elongated portion (fig. 109). The cell wall of the elongated portion which is to become the holdfast is comparatively thick.

The number of chromosomes at prophase (figs. 110, 111) and seen in polar view at metaphase (fig. 114) is 48. The axis of the figure is often perpendicular to the growing axis of the sporeling (fig. 113). After telophase the sporeling is divided into two cells (fig. 115). The nuclei of the two cells divide one after the other; sometimes the lower nucleus increases more rapidly than the upper (fig. 117), or the upper nucleus begins to divide first (figs. 116, 118–120). In sporelings consisting of three cells, mitosis occurs in various order in the three nuclei; the nucleus of the basal cell may divide first (figs. 121, 122), or the three nuclei may divide simultaneously (fig. 123). The number of chromosomes appearing at the prophase (figs. 121, 123) is 48.

The fourth, fifth, and subsequent divisions, that occur continuously for more than ten days, multiply the number of the cells of the sporeling, resulting in the development of the upright columnar form that grows standing upon the substratum, and then the direction of growth becomes changed.

Before describing this change of growth which occurs in sporelings about ten days old, we shall note briefly the fate of the red pigment that is conspicuous in the living gametes. As was stated before, the red pigment is always associated with the plastid. A part of the plastid becomes impregnated with some substance of a deep orange color, which seems to disorganize instantly with the death of the sporeling. The most interesting point is that the cilia are attached to the pigment, and the red pigment is the only structure within the sporeling that bears any close and direct physical connection with the cilia. Moreover, the plastid that bears the red pigment always lies near the nucleus. By the union of male and female gametes the red pigment bearing plastid of the male gamete is introduced into the female gamete and consequently

two red pigment structures are always present in sporelings resulting from fertilization: a large red pigment spot is associated with a large plastid of the female gamete, and a small red pigment spot upon a small plastid is characteristic of the male gamete. Although the plastid bearing the red pigment of the male gamete grows in size after its introduction into the cytoplasm of the female gamete, yet it seldom becomes equal in size. This difference in size of the two pigment spots is maintained as far as the present observation goes. Fig. 9 represents some of the stages in the development of sporelings from the 1-celled to the 5-celled stage, indicating the various positions of the two red pigments of male and female origin. The red pigment was recognizable even up to the 16-celled stage, and beyond the 20-celled stage it becomes hard to recognize, probably on account of the disintegration of the coloring matters. It seems probable that the red pigment is concerned with the motility of the gamete rather than with fertilization.

As stated before, the sporelings develop continuously in one direction, and as a consequence after about ten days there is produced a columnar structure standing upright upon the substratum, and then the direction of the growth becomes changed. Cells of the basal portion of the columnar sporeling divide laterally, instead of in the direction of the axis of the growth, so that by repeated cell division there is produced a flat expansion, the whole structure of which might be well compared with a candlestick, the candle being the column and the base the newly developed flat expansion. The basal expansion is developed by the repeated periodic cell divisions on the lateral margin, which causes a zonation like that in *Peyssonnelia;* besides, the thallus is characterized by intercalary growth. Sporelings at about 20 days after fertilization are shown in fig. 10, *a*. Later the upright column does not seem to grow much, only the basal expansion continuing to develop. Sporelings 30 days old are shown in fig. 10, *b*. In 55 days old sporelings, the growth of the column has ceased, and it remains small, hardly recognizable to the naked eye, while the basal expansion reaches a considerably larger size and becomes well fitted to flourish as an independent creeping structure (fig. 10, *c*, *d*).

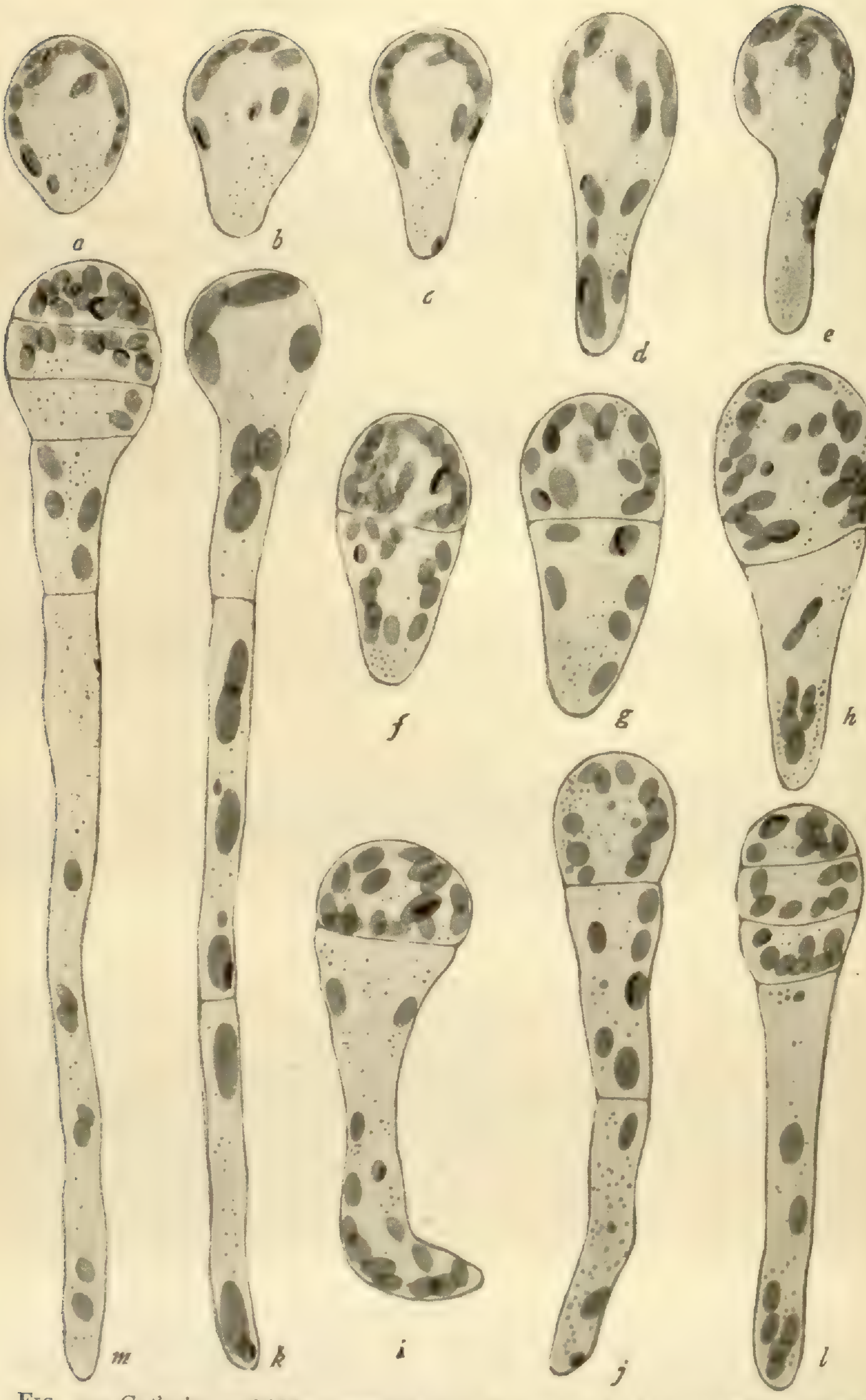

FIG. 9.—*Cutleria multifida:* normal sporelings sketched from living material; *a–e*, one-celled stage; *f–i*, two-celled stage; *j* and *k*, three-celled stage; *l*, four-celled stage; *m*, five-celled stage; nucleus not recognizable in living material; the two pigment spots associated with plastids are of maternal and paternal origin; the small pigment spot introduced by the male gamete, the large one by the female gamete; the plastid that bears the small red pigment spot has increased in size after its introduction into the female gamete.

FIG. 10.—*Cutleria multifida*: normal sporelings; *a*, 20 days after fertilization; *b*, 30 days after fertilization; *d*, 55 days after fertilization (*d* represents a part of a sporeling under the same magnification as *a* and *b*, and the whole sporeling is shown in *c*); the vertical column which is the result of primary growth of the sporeling has not grown since 30 days after fertilization, and the zonal horizontal expansion at the base of the column begins as a secondary structure and develops into the characteristic *Aglaozonia* form, as shown in *b* and *c;* compare with fig. 11.

The similarity of the habit of this creeping expansion of the thallus to that of *Aglaozonia* in nature is striking. The material of *Aglaozonia* collected fresh from Posilipo and Nisida, which has grown creeping on a sea-urchin's shell or on the rock, showed a number of forms in various stage of development. If the creeping expansion of the thallus obtained in cultures is compared with *Aglaozonia* of similar size as it occurs in nature, it is hard to find any difference in their appearance. Not only the zonal growth and occasional intercalary growth of the thallus is alike in these two forms, but also the cell structure as seen in sections under the microscope is remarkably similar in the two forms. The nuclei of the thallus obtained in culture contains 48 chromosomes, and the same number is present in *Aglaozonia* as it occurs in nature.

The author's cultures of the thallus expansion, the *Aglaozonia* form of *Cutleria*, were not continued up to the stage of producing reproductive organs.

GERMINATION OF THE UNFERTILIZED FEMALE GAMETES

As was described before, the female gametes after their escape from the gametangia may swim for as long a time as 2 hours, or for as short a time as 5 minutes. When the motion becomes sluggish, the body becomes spherical, the plastids which have hitherto occupied the more posterior portion of the body become irregularly scattered throughout, and finally the cilia are either withdrawn or they coalesce with the plasma membrane as the movement ceases. If the female gametes in this condition are kept with no addition of the male gametes, they remain dormant for a considerable time. The female gamete left in this condition at length shows a change in the outermost layer of the plasma membrane that is in direct contact with sea water, the change resulting in the development of a cell wall, thin at first, and then increasing in thickness. The nucleus is in the resting condition (fig. 124). Not infrequently it is observed that the female gamete, now inclosed within a cell wall, has an elongation at a part of the body where the cell wall is thickened (figs. 125, 8, *d*).

This unfertilized female gamete commences to divide 24–28 hours after it has assumed the quiescent condition. The mitosis

occurs frequently without any elongation of the sporeling. When the nucleus is in prophase there seems to be no departure from the typical mitosis characteristic of *Cutleria*, the division being perfectly normal. The number of chromosomes appearing in prophase is 24 (fig. 126). At metaphase two centrosome-like structures appear at the poles (fig. 127), and the number of chromosomes is clearly 24 (fig. 128). Sometimes the metaphase is reached while a part of the sporeling is elongating (fig. 130). The chromosomes split longitudinally and half of each chromosome passes to each pole (fig. 131). The axis of the first mitotic figure may be either longitudinal or transverse to the axis of the sporeling (figs. 132, 133). After telophase two new daughter nuclei are formed (fig. 134). In the sporeling of the unfertilized female gamete beautiful radiations are closely associated with the upper nucleus (fig. 135), but they are of short duration, and disappear completely when the nucleus passes into prophase (fig. 136). When the upper nucleus is in metaphase (fig. 137), the lower nucleus enters into prophase. Both the metaphase, viewed from pole (fig. 137), and the prophase show 24 chromosomes. One peculiarity observed is the appearance of elongated chromosomes in the upper nucleus of a 2-celled sporeling during prophase (fig. 138). The division of the upper and lower nuclei is not simultaneous; sometimes the upper nucleus is far ahead of the lower, so that the former is in late telophase

FIG. 11.—*Cutleria multifida:* apogamous sporelings: *a*, 30 days after germination; *b*, 50 days after germination; *d*, 75 days after germination (*d* represents a part of a sporeling under the same magnification as *a* and *b*, and the whole of the sporeling is shown in *c*); the apogamous sporelings are slow in development as compared with the normal ones, and assume massive forms at first and then the flat zonal expansion like the normal ones.

while the latter is in metaphase (fig. 140), or the upper is left behind in the resting state while the lower is in anaphase (fig. 139). In sporelings of the 3-celled stage the lowest nucleus may divide (figs. 141, 143) in advance of the rest, or the middle one may divide first (fig. 142).

Cell divisions continue up to a 12–22-celled stage (figs. 144–146). As seen in fig. 146, the axis of growth does not continue in one direction, as in normal fertilized sporelings, but the structure is branched. After repeated divisions there is formed a somewhat upright structure, not columnar, but rather laterally produced and in irregularly massed lumps (fig. 11, *a*). This upright structure with a lateral uneven mass consisting of about 35 cells is produced in 30 days. The irregular nature of this structure is still seen in sporelings of 50 days (fig. 11, *b*). Some of the irregular appendages of the structure which happen to be in contact with the substratum become creeping expansions and later become the main part of the sporeling.

And thus the unfertilized sporelings after 75 days develop into the thalloid creeping structure (figs. 11, *c*, *d*), and the product bears some resemblance to the product of the sporeling resulting from a fertilized gamete. Comparing these two products, the points of marked difference are as follows: (1) the first segmentation division occurs 6 hours later than in the normal sporeling; (2) the subsequent growth of these sporelings is very much slower than in normal sporelings; (3) unfertilized sporelings are characterized by developing into irregular masses at first, and even after they have assumed the expanded structure, they still show a tendency to form massed appendages; (4) the number of chromosomes is unchanged, the sporeling from the unfertilized gamete containing only 24 chromosomes.

Aglaozonia reptans

MITOSIS IN THE VEGETATIVE CELLS

Aglaozonia reptans Crouan has a creeping crustaceous habit on rock or sea-urchin's shells, attached by rhizoidal holdfasts from the superficial layer of the ventral surface. The superficial layer consisting of small cells of equal size is either single (fig. 147) or

double (fig. 148) on the dorsal surface, and between the dorsal and ventral superficial layers there are two or three layers of parenchyma-like cells of huge size. Any cells in the superficial layer of the dorsal surface of young *Aglaozonia* are favorable for studying vegetative mitosis.

The vegetative mitosis was studied chiefly in the nucleus of the superficial cells of *Aglaozonia*. The main features of the division are similar to those of *Cutleria*, and consequently a detailed account and figures will be omitted at this time, but a few points should be noted.

The size of the nucleus in the superficial cells is either about the same as that of the plastids within the cell or is even smaller. When the nucleus is in the resting state, the chromatin network is remarkably similar to that of *Cutleria*, the chromatin knots being a conspicuous feature, though few in number, while the fibrils are very scanty and broken. One noteworthy feature not common in the case of *Cutleria*, but of general occurrence in *Aglaozonia*, is that deeply stained granules about the size of the chromatin knots within the nucleus are present around and close to the membrane outside the nucleus. These granules become faintly stained and evidently diminished in size during the mitotic phase within the nucleus, and they entirely disappear while the nucleus is still in prophase. It seems probable that the granules may be material allied to chromatin that might have passed into the nucleus, thus contributing to the formation of chromosomes.

The chromosomes appearing in prophase are 48 in number, and their form is in nothing different from those of *Cutleria*.

FORMATION OF ZOOSPORANGIA

Zoosporangia are produced on the upper surface of the thallus. When living *Aglaozonia* is viewed from above, the groups of zoosporangia are distinguished by patches of darker color, contrasting sharply with the light brownish olive color of the sterile portion. These patches are composed of hundreds of thousands of zoosporangia which are produced in palisade arrangement upon the thallus. The details of the origin of the zoosporangium are as follows: a superficial cell of the thallus elongates slightly and

divides, giving rise to two cells, the upper one of which becomes a zoospore mother cell, and the lower remains as a stalk cell (figs. 148, 149). The process occurs in a number of superficial cells lying side by side, and as a consequence zoospore mother cells are produced in great numbers, lying close together and parallel. When the superficial layers are double, the cells in the outer layer elongate

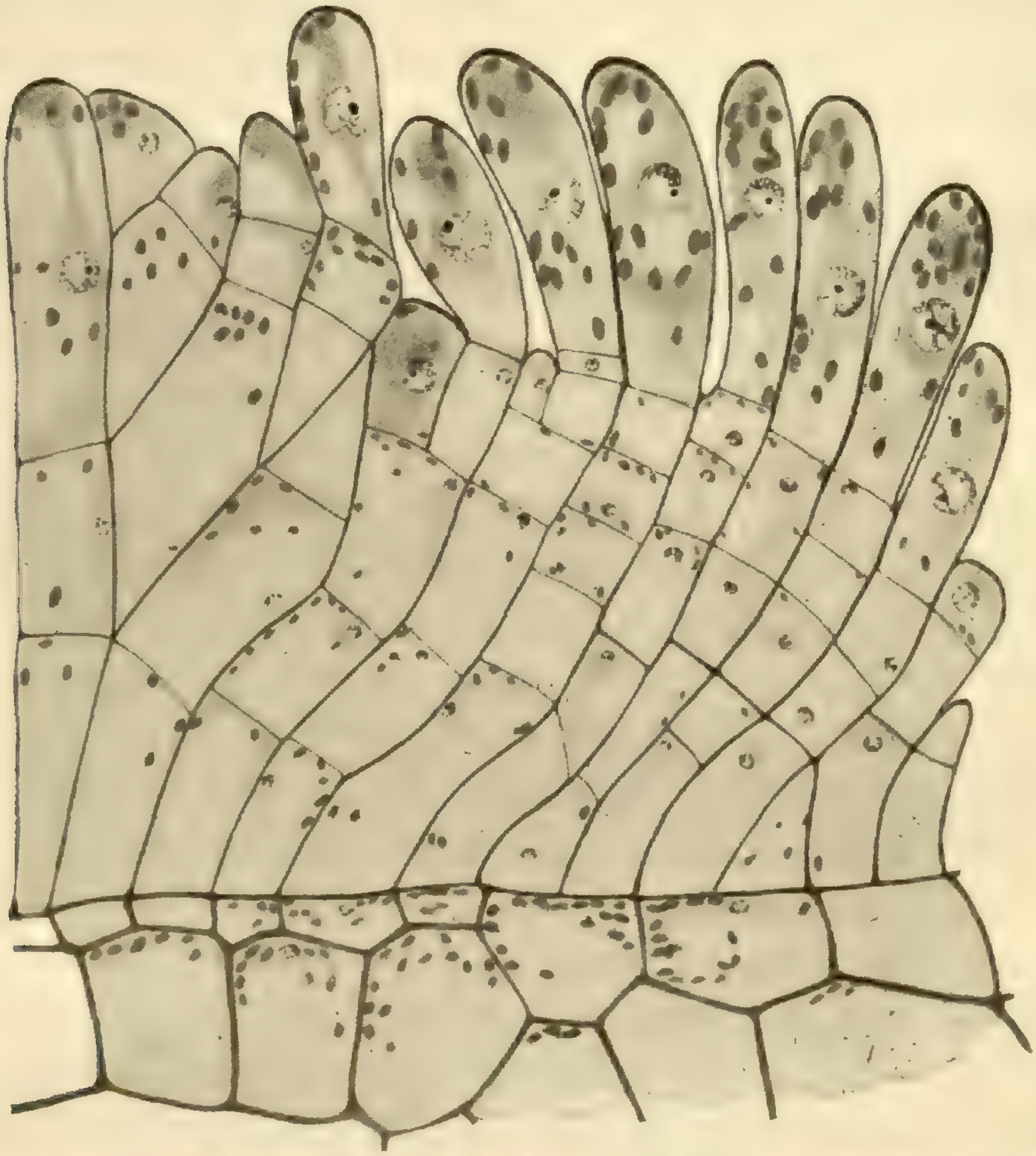

FIG. 12.—*Aglaozonia reptans:* portion of a thallus with numerous filaments; the filament usually consists of two cells, but in the present exceptional case they are made up of a varying number of cells (3–7), and their terminal cells are zoospore mother cells.

and directly become the mother cells (fig. 150). Not infrequently it is to be observed that several cell divisions take place in the superficial cells, so that a single superficial cell develops into a slender filament consisting of 3–7 cells, and the terminal one becomes the mother cell (fig. 12). The zoospore mother cell is at first like an ordinary superficial cell, with length and breadth about equal

(fig. 151), but sooner or later the cell begins to elongate upward until its length becomes three times its width, the top being slightly swollen and the base narrowed. The nucleus lies either in the center or a little above the middle of the cell. The cytoplasm is full of vacuoles of various sizes, and plastids are quite numerous.

The nucleus in the resting condition contains a moderate amount of chromatin network and a nucleolus. The network is composed of very small chromatin knots and irregular fibrils (fig. 152); the proportionate amounts of the knots and fibrils seem to interchange at this stage (fig. 153). In iron-hematoxylin preparations dark kinoplasm surrounds the nucleus (figs. 151, 152). The amount of the chromatin gradually increases and the general tendency is for the broken fibrils to become thicker and continuous, transforming the knots into the fibrils (fig. 154). At this time, a single (figs. 154, 158) or double (figs. 155, 157) centrosome-like structure with radiations is recognizable at the poles.

Stronger and more continuous threads are then established by the rearrangement of the knots and fibrils. The chromatin network, which is composed of a number of broken threads of various lengths and thicknesses, now entirely devoid of former knots, is not very great in amount. For a while the broken threads are seen running for quite a distance either close to the membrane or traversing the cavity (fig. 159, 160). Then the threads gradually become more and more uniform in thickness and are transformed into somewhat regularly arranged loops, centered at a certain part of the cavity (fig. 161). This transformation represents the beginning of the synaptic stage.

This bunch of loops may be in regular arrangement (fig. 162) or adhering at the base to the membrane and diverging upward so that each loop passes along the membrane (fig. 164); or often each loop of the bunch differs in compactness of structure, and consequently some loops are short while others extend for some distance (fig. 165). In any event, a cross-section at these stages shows that the number of the cut ends of the arms of all the loops is about 48 (fig. 166). These loops now shorten considerably (fig. 167) and some of them are soon detached from the main group and form paired chromosomes (figs. 168, 169), and finally there are established 24 bivalent

chromosomes, each derived from one of the loops (fig. 170). These 24 bivalent chromosomes gather near the center of the nucleus (fig. 171), and then are arranged at the equatorial plate (fig. 172), when the number is clearly counted in the polar view (fig. 173). Then each of the chromosomes splits longitudinally (fig. 174) and half of each proceeds to each pole of the spindle and there again the polar view of the anaphase clearly shows 24 chromosomes (fig. 175). The chromosomes grouped at the poles now become closely applied to one another (figs. 176, 177) and finally there are organized two daughter nuclei (fig. 178). Up to this phase a kinoplasmic mass persists, either surrounding the nucleus or near the pole of the spindle, but centrosome-like structures are recognizable only at metaphase.

The two newly formed daughter nuclei now increase in size. Their relative position within the cell is variable; sometimes they are wide apart (fig. 180), and often they lie for a while in close contact (fig. 182). The centrosome-like structure with radiations is present, associated with the two resting nuclei (fig. 180). These two nuclei may divide simultaneously or in succession (figs. 183–185). The number of chromosomes present during this division is also 24, and with this reduced number the nuclei pass into telophase (figs. 186–188). The third division follows the second after a short rest, 24 chromosomes being present at metaphase (fig. 189). As a result of the third division there are produced eight nuclei within the mother cell (fig. 190).

It is interesting to note the relative position of the axes of the mitoses that occurred within the mother cell. Only a few of the cases are represented in fig. 13. As the figures clearly show, the axis of the first mitotic figure is either in the direction of the long axis of the mother cell, or slightly oblique to the axis; in some cases the axis is still more oblique, until finally the axis of the figure is perpendicular to the long axis of the cell. In the second mitosis, considering the cases where the two mitotic figures occur at the same time, the relative position, as shown in figures, shows all possible directions of the axes. The same is true of the third nuclear division. All of these zoospore mother cells show no polarity in regard to the axis of the mitotic figures.

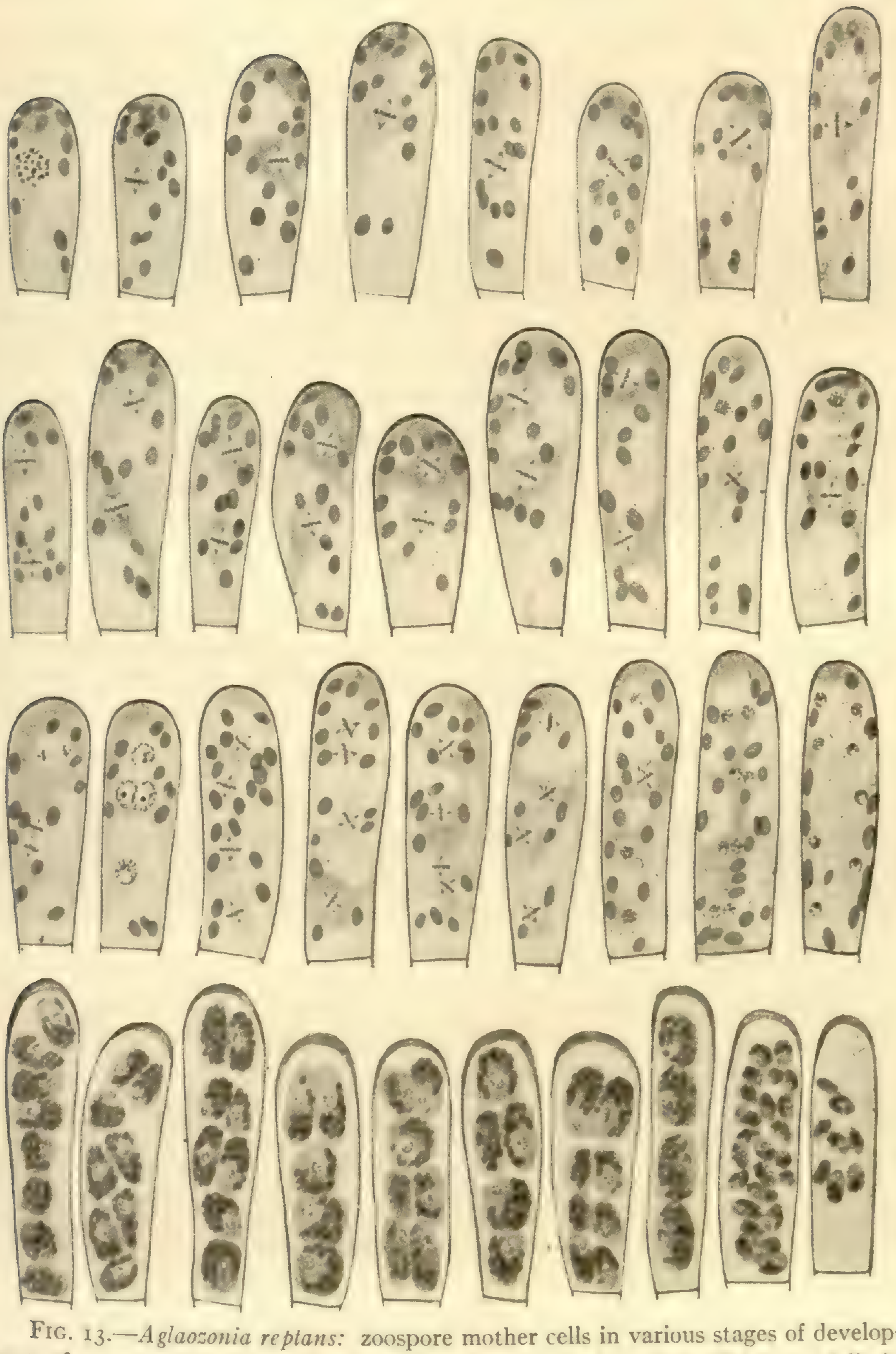

FIG. 13.—*Aglaozonia reptans:* zoospore mother cells in various stages of development; first row, the nuclear figures are in metaphase of the first division and lie in various positions in relation to the axis of the mother cell; second row, metaphase of the second division; third row, two at the right in anaphase and telophase of the second division; third row, two at the right in anaphase and telophase of the second division, two at the left in 8-nucleate stage, and the rest in metaphase of the second division; fourth row, various arrangements of zoospores formed within the mother cells, the two at the left are the two sections of a single mother cell which contains 32 zoospores, and in the rest 8 zoospores are present.

The plastids in the zoospore mother cell seem always to be multiplying in number during these nuclear divisions. When the nucleus is in prophase of the first division, the surrounding cytoplasm contains a number of plastids in various stages (fig. 191); the number is increased at the time of the 4-nucleate stage (fig. 192), and at the 8-nucleate stage the cell is filled completely with the plastids (fig. 193). It seems probable that this gradual multiplication of plastids may be one of the reasons why the zoospore mother cell constantly increases in size up to the formation of the zoospores, when the length of the mother cell becomes six times its width.

When the zoospore mother cell has reached the 8-nucleate stage, cleavage furrows generally occur in the cytoplasm, and divide the contents of the mother cell into 8 zoospore primordia (*Anlagen*). Not infrequently, however, one or two more divisions occur after the third, and as a consequence there are produced 16 or 32 nuclei, and in those casés 16 or 32 zoospores are formed (fig. 13).

The mechanism of the cleavage of the cytoplasm within the mother cell in the formation of the zoospores is noteworthy. The plastids at this time are arranged mostly near the cell membrane, and the central part of the cell is occupied by the vacuolated cytoplasm (fig. 194). The nucleus lies either near the periphery or in the midst of the cytoplasm. There is first a movement of the nuclei, and this is followed by a movement of the plastids; that is, the 8 nuclei are distributed to certain portions, not very close to the periphery, and then a number of the plastids move toward one of the nuclei as a center and surround it (fig. 195). Then there begins the separation of the *Hautschicht* from the cell wall, and at the same time cleavage furrows appear in the cytoplasm between the nuclei; the formation of the furrow is initiated by small vacuoles arranged in a cleavage line, which unite afterward and break up, leaving the furrow in their places (fig. 196). As the result of the process of the cleavage furrow, there are produced free independent zoospore primordia packed close together within the mother cell (figs. 198, 199). The relative position of the zoospores thus produced is determined by the position the nuclei had occupied before the cleavage began. Some of them are shown in fig. 13.

During the development of the zoospore mother cell, while these nuclear divisions have been taking place, the cell wall remains apparently unchanged, except at the top of the mother cell, where there has been a gradual increase in thickness, which culminates at the time of cleavage. As the zoospore primordia are completely formed, the top of the cell wall begins to swell (fig. 200), then disintegrates into lamellae, with lacunae between them (figs. 201, 202). Finally the disintegrating lamellae of the cell wall become completely disorganized, so that a pore is formed at the top, and through this the zoospores escape after maturity.

The zoospore in free swimming condition is oval (fig. 14, *a*), and usually contains more than 20 plastids. Associated with one of the plastids, which lie inside the plasma membrane, there is a red pigment spot, in close association with which two cilia of different lengths are attached, the longer one being directed toward the anterior end, about three times the length of the zoospore, and a short one extending in the opposite direction about one and one-third the length of the zoospore. The length of the zoospore is 22.5 μ when the output of the zoospores in a cell is 8 (figs. 14, a', a''), 18.7 μ when the output is 16 (fig. 14, *b*), and 10.5 μ when the output is 32 (fig. 14, *c*).

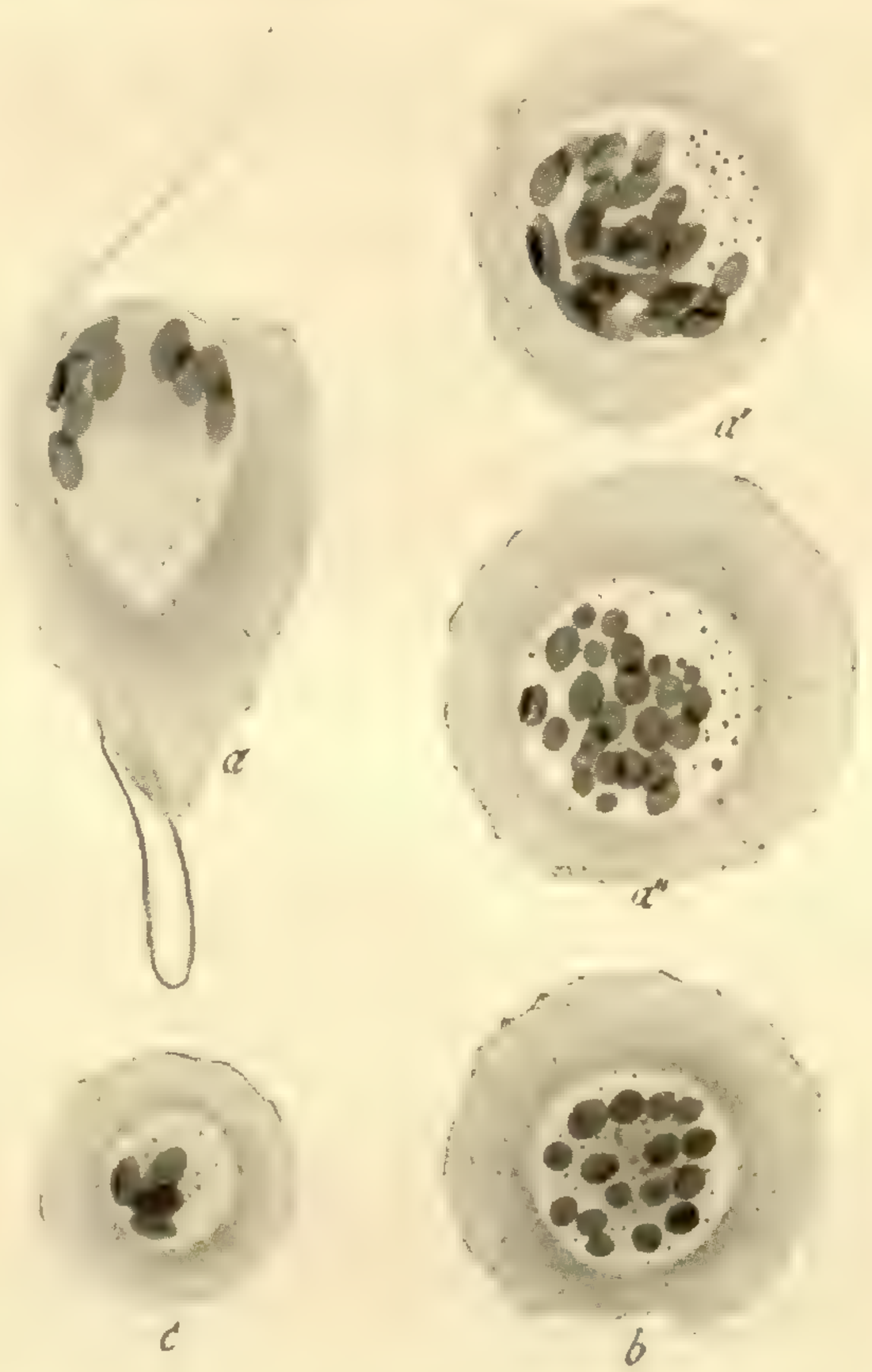

FIG. 14.—*Aglaozonia reptans:* zoospores sketched from living material; *a*, in free swimming condition; *a'*, beginning to be quiescent and spherical; *a''*, in quiescent condition; the size varies according to the number of nuclear divisions within the mother cell; *a*, *a'*, and *a''* are the products of three divisions (output of 8 zoospores); *b*, from four divisions (output of 16 zoospores); *c*, from five divisions (output of 32 zoospores).

GERMINATION OF THE ZOOSPORE

The duration of the motile condition of the zoospores varies; some ceased to be motile within 10 minutes, while others were still moving after more than 90 minutes; but in any case, when the zoospore becomes sluggish, the body gradually becomes spherical and the cilia are withdrawn or become coalescent with the plasma membrane.

About two hours after the quiescence of the zoospore, the outermost layer of the plasma membrane becomes changed into a delicate cell wall. The nucleus at this time is in the resting condition, with a centrosome-like structure and radiations near the nuclear membrane (fig. 203). This condition remains unchanged during the next 20 hours (fig. 204). The presence of centrosome-like structures and radiations is not a definite feature; at about 24 hours after quiescence they may (figs. 206, 207) or may not be visible (figs. 205, 208).

The first segmentation division of the germinating zoospore takes place 24 hours after its quiescence. The nucleus enters prophase either at the center of the cell (fig. 209) or in its elongated part (fig. 210), and when the chromosomes are arranged at the equatorial plate (figs. 211, 213), two centrosome-like structures are present at the poles. The polar view of the metaphase shows distinctly 24 chromosomes (figs. 212, 214). Each of the chromosomes divides longitudinally and half of each passes to each pole (fig. 215). The second mitosis in these two nuclei may occur in succession (figs. 217–221) or simultaneously (fig. 222), but in either case 24 chromosomes can be counted at prophase and in polar view of metaphase.

In the zoosporelings consisting of three cells the three nuclei divide in various order (figs. 224, 225), and in prophase of any nucleus 24 chromosomes are present. In the further nuclear divisions in the development of the zoosporelings the same number of chromosomes is counted. This young sporeling after a multitude of cell divisions (figs. 226–228) develops into a long filamentous structure instead of a stout column. The product at about the end of 20 days after germination is shown in fig. 15, *a*. In habit the sporeling is very like the young filamentous stage of *Cutleria*.

Later this filament does not continue in the upward direction, but there appears a new lateral structure near the basal region of the primary filament, and the whole structure clings to the substratum with rhizoids which grow from the base; thus, contrary to the behavior of the fertilized gamete of *Cutleria*, basal expansions that creep flat upon the substratum are never found. The plant at 30 days is illustrated in fig. 15, *b*, which resembles the young *Cutleria* as found in nature.

The new structure thus initiated laterally from the basal region of the primary filament grows in such a way that it finally meets the other side of the primary filament so as to form a funnel which is expanded upward and narrowly constricted downward. Upon the expanded upper margin of this funnel-shaped structure delicate hairs begin to grow. This stage is reached in about 40 days (fig. 15, *c*). These funnel-shaped structures obtained in the artificial culture present a striking resemblance to the young plants of *Cutleria* in nature as they occur in tufts on the rock or on shells. One difference is that the young plant of *Cutleria* in nature, at the same stage as the cultures in the

FIG. 15.—*Aglaozonia reptans:* zoosporelings; *a*, 20 days after germination; *b*, 30 days after germination; *c*, 40 days after germination; the sporelings are filamentous in primary growth as shown in *a*, then gradually assume the funnel-shape shown in *b* and *c*, this shape being characteristic of the young stage of *Cutleria* in nature.

laboratory, is furnished with a luxurious display of long beautiful hairs on the margin of its funnel-shaped thallus, while such a hairy growth has not yet been seen in cultures. It must be admitted, however, that there is a difference between conditions in nature and in cultures which may account for the difference in this character; the young plant of *Cutleria* is found on the rock at a depth of 1–5 meters, while the culture was kept in a tank where the water was never deeper than 6–8 inches. Intensity of light, temperature of water, its pressure, its movement, and other factors may be quite different, and yet in spite of such a difference of external environment, the zoosporelings of *Aglaozonia* developed into erect structures of funnel-shape as in the young *Cutleria* plants, and fundamentally different from the flat creeping expansion habit of both parent forms and of the plants resulting from fertilized female gametes of *Cutleria*.

The young plants of *Cutleria* and the product of the zoosporelings of *Aglaozonia* in culture show not only the common habit in their development and similarity in their outer morphological characters, but also a similar cell structure, similar nuclear conditions, and the same number of chromosomes.

Discussion of cytological phenomena

THE ORIGIN OF UNIVALENT CHROMOSOMES

The chief constituents of the resting nucleus of *Cutleria* and *Aglaozonia* are the network and nucleolus. The network is composed of two parts, granules and irregular fibrils in varying proportions. The granules are of different sizes and some of them are connected by very slender, irregular fibrils, or lie isolated usually near the nuclear membrane. The number of granules in the nucleus quite often, though not always, corresponds more or less to the number of chromosomes. The granules may be extremely small, but the preparations never fail to show their presence. Both granules and fibrils consist of chromatin.

As a rule, there is only one nucleolus, and it lies quite free from the nuclear network, with which it shows no visible physical connection. Concerning the morphological function of the nucleolus in algae, STRASBURGER (**55, 57**) published the view that the sub-

stance of the nucleolus is utilized for spindle formation, the conclusion being drawn from the fact that the nucleolus disappears partly or completely immediately preceding the formation of the spindle. WILLIAMS (**66**) in his study of *Dictyota* accepted this view. STRASBURGER (**53**) had held the opinion that the nucleolus was reserve material serving to build up the chromosomes, and this view was followed by SWINGLE (**61**) on *Stypocaulon* and by MOTTIER (**32**) on *Dictyota*. The view that the chromosomes are formed directly from the nucleolus was supported by TANGL (**62**), MEUNIER (**29**), MOLL (**30**), DECAGNY (**10**), HENNEGUY (**19**), VAN WISSELINGH (**67–69**), BERGHS (**3**), KARSTEN (**22**), and TRÖNDLE (**64**) in their studies of *Spirogyra*, by WOLFE (**70**) on *Nemalion*, by LEWIS (**27**) on *Griffithsia*, and by SVEDELIUS (**60**) on *Delesseria*. These investigations differ greatly in regard to exactness and details. In some of these papers views are expressed with adequate illustrations, but often the illustrations and text are quite contradictory, and frequently the figures would afford better support to some other interpretation. In their statements, however, these authors seem to agree that some or all of the chromosomes are organized directly from the material of the nucleolus, which in this way either may be used up partly or even entirely.

A fourth opinion is that the chromosomes arise exclusively from the chromatin network, the nucleolus taking no direct part in their development. *Fucus* illustrates the situation. The plates accompanying the studies on *Fucus* by STRASBURGER (**56**), and by FARMER and WILLIAMS (**15**) show this situation, and more details have been furnished by the present author (**73**). *Polysiphonia* (YAMANOUCHI **71**), *Corallina* (DAVIS **8,** and a forthcoming paper by the author), *Zanardinia* (YAMANOUCHI **76**), as well as *Cutleria* and *Aglaozonia*, present a similar situation.

THE ORIGIN OF BIVALENT CHROMOSOMES

Contrasted with the formation of univalent chromosomes in typical mitosis, the origin of bivalent chromosomes is rather complex. As already described, in the resting nucleus of the zoospore mother cell of *Aglaozonia* the chromatin network is composed of granules and fibrils. While in typical mitosis the network finally

becomes transformed into isolated individual chromosomes, the granules and fibrils being entirely used up in the formation, in the reduction mitosis the granular parts become transformed into fibrils, and consequently during the presynaptic stage there are only thread structures within the nucleus. These chromatin threads, at their beginning irregularly thickened and branched, become much evener, and the transformation continues until long continuous threads are formed, which run freely throughout the cavity. The threads thus formed, from the beginning of their transformation to their completion as continuous structures, have a single nature. Entering the synaptic condition, the single threads then shorten and thicken, and become either eccentrically grouped as a loose tangled mass at one side of the nuclear cavity, or are variously scattered all over the membrane. The threads eventually form loops by repeated folding. The number of loops is 24. Each loop folds together at its bent end so that the bent arms come into contact with each other in the culmination of synapsis. As they emerge from synapsis, there are present 24 bivalent chromosomes, which become detached from the nuclear membrane, moving toward various parts of the nuclear cavity.

The rélationship of the chromatin threads in prophase, the loops in synapsis, and the bivalent chromosomes of postsynapsis have been clearly traced. A pair of bivalent chromosomes corresponds to one of the loops in synapsis, the loop being formed by a folding back of the chromatin thread, so that a loop in synapsis should be considered as composed of two sporophytic chromosomes associated end to end. The two elements of the bivalent chromosomes separate from each other at the metaphase of the first reduction division, thus effecting what may be regarded as a qualitative reduction.

The origin and behavior of bivalent chromosomes as described for *Fucus* (**73**) and *Zanardinia* (**76**) agree perfectly in essentials with the present account of *Aglaozonia*. For example, figs. 161, 162, and 172, illustrating looping threads in synapsis and chromosomes in late prophase in the zoospore mother cell of *Aglaozonia*, when compared with figs. 43, 44, and 49 illustrating similar stages of *Fucus* (**73**), demonstrate at once their similarities.

Disregarding many points which may differ in particulars, the case of *Aglaozonia*, in which bivalent chromosomes in seemingly reduced number have originated by the folding back of sporophytic chromosomes united end to end, will agree in essentials with observations made by different authors on various forms, for example, by FARMER and MOORE (**13, 14**), SCHAFFNER (**52**), and MOTTIER (**34**) on *Lilium*, by STRASBURGER (**58**) on *Galtonia*, and by one group of zoologists, such as VON RATH (**37**) on *Gryllotalpa*, RÜCKERT (**41**) on copepods, and MONTGOMERY (**31**) on *Peripatus*.

In general, while the method of forming bivalent chromosomes by the end to end fusion of sporophytic chromosomes or *métasyndèse*, as GRÉGOIRE (**17**) calls it, occurs in *Fucus*, *Zanardinia*, *Aglaozonia*, and other forms, there is also another method by side to side fusion, or *parasyndèse*, in *Polysiphonia* (**71**), *Nephrodium* (**72**), *Osmunda* (**75**), and various other forms, such as *Lilium* (GRÉGOIRE **16,** BERGHS **2,** ALLEN **1**), *Allium* (BERGHS **2**), *Trillium* (GRÉGOIRE **16**), and *Drosera* (ROSENBERG **40**). From these observations it is evident that in the former class there is no duality in the formation of thread structures (*leptotènes*) from the resting nucleus, and therefore in synapsis the two bent arms of a single loop come into close association; and in the latter class, a duality is present at the time of the beginning of the thread structures (*leptotènes*), and the two independent members of the duality come into contact during synapsis. In both classes, each of the two elements of the bivalent chromosome is derived from a single sporophytic chromosome, and the two elements separate in the first division. It seems highly probable that there are two distinct types of arrangement of sporophytic chromosomes at synapsis in plant cells.

POLAR ORGANIZATION

Views on the polar organization of plant cells are conflicting. Some of the algae present clear evidence of such polarity, the best known examples being *Stypocaulon* and *Sphacelaria* (**61**), which have a center in the form of an aster with a centrosome at the side of the resting nucleus of the apical cell. The centrosome is said to divide previous to each mitosis, to establish the poles of the spindle. A similar centrosome with radiations is present in the

tetraspore mother cell of *Dictyota* (**32, 66**). Other algae, such as *Corallina* (**8**), *Fucus* (**15, 56, 73**), *Polysiphonia* (**71**), show highly advanced centrospheres at the poles of the spindle; but investigators claim that in *Corallina* and *Polysiphonia* they appear simultaneously at the two poles during prophase, culminate at metaphase, and disappear at anaphase or telophase; and in *Fucus* one of them appears before the other and they disappear at telophase; only as rare cases they remain recognizable at the side of the resting nucleus. Thus, so far as present knowledge goes, the persistent continuity of polar organization in algae cells has not been demonstrated through successive cell generations.

The subject of polar organization has received especial attention in HARPER'S studies on mildews, especially *Phyllactinia* (**18**). In this form, the "central body" lies within the membrane of the resting nucleus, and it is connected with chromatin strands so as to give polarity to the nucleus. The poles of the spindle are formed by division of the central body. HARPER believes in the permanence of this structure from mitosis to mitosis, and in the persistence of its connection with chromatin.

The studies of recent years on the cells of pteridophytes and spermatophytes have failed to support certain claims for the presence of centrosomes and have indicated that their cells are without visible polar organization. MARQUETTE (**28**) published the view that the presence of polarity in the leaf cell of *Isoetes* is manifested by a large starch-containing body that lies closely pressed against the side of the nucleus. Previous to nuclear division, according to MARQUETTE, the polar structure divides, and during mitosis the structure persists up to telophase, and finally one of them remains at the side of the newly formed daughter nucleus, and a similar constriction division occurs in the structure previous to the next nuclear division. He also found a polar organization of the spore mother cell of *Marsilia*, in the form of aggregated starch grains, conspicuous at the time of synapsis, but disappearing just before the formation of the first spindle; the organization is of very short duration, not continuing throughout the mitosis.

In *Cutleria* and *Aglaozonia*, polar organization is manifested by the appearance of centrosome-like structures with or without

radiations, always only at metaphase, and as a rule completely disappearing at telophase. It may be found that polarity does not depend in all cases upon the presence of permanent protoplasmic structures of recognizable size or upon such morphological differentiation as to rank as organs of the cell. There may possibly be polarity at times without visible protoplasmic organization, but so far as the visible organization of the cell is concerned, there seems to be no permanent polar organization in the cells of *Cutleria* and *Aglaozonia*. The transient polar organization is formed *de novo* at each mitosis in every possible position about the nucleus. The variability of the polar axis of the mitotic figure demonstrates the feature (fig. 13).

Zoospores and gametes of algae invariably present a conspicuous polarity in that their cilia are situated at one end or at a definite point on the side, the point of insertion being devoid of plastids. The most vital problem of zoospore and gamete formation is whether the polar organization of these cells arises *de novo* at the time of development or is handed down from the succession of the cells that are their progenitors. STRASBURGER (**57**), from his studies of the zoospores of *Oedogonium*, *Cladophora*, and *Vaucheria*, decided that the cilia bearing organ, the blepharoplast, arises in the plasma membrane (*Hautschicht*), the nucleus lying in close association at the time of its formation. MOTTIER (**33**) later described a similar origin of the blepharoplast in *Chara*. DAVIS' work on *Derbesia* (**9**) showed that the blepharoplast is developed at the plasma membrane in the form of a ring that has been organized by the side by side union of numerous granules arranged in a circle. The marked polarity is manifested after the appearance of the granules.

The details of the organization of zoospores and gametes of *Cutleria* and *Aglaozonia* have not been given in this account because the subject will be dealt with in a special paper treating of the origin of motile sperms or spores of algae, such as *Fucus*, *Zanardinia*, *Ectocarpus*, and of some green algae, so that a brief account will be sufficient for the present consideration of polarity.

In the zoospore mother cell stage, which is usually reached at the 8-nucleate stage of the zoosporangium, cleavage furrows start

from the periphery and cut into the protoplasm in the form of curved and branching furrows. Finally, the protoplast within the sporangium becomes divided into approximately equal masses, each of which contains a single nucleus. These masses are zoospore primordia, and each develops into a uninucleate zoospore. The nucleus lies first at the center of the zoospore primordium, with plastids lying near the periphery of the cell. The polarity of the cell is clearly established when the nucleus moves toward the peripheral region of the cell, displacing all the plastids in the vicinity, except one which remains near the nucleus. At this time a small granule can be seen lying in the plasma membrane near the nucleus. This granule becomes the blepharoplast, and in a part of the body of the plastid remaining near the nucleus there is later developed a red pigment which makes it look as if the cilia had arisen from the red pigment.

Thus the polarity of the zoospore is manifested only after the organization of the blepharoplast and red pigment spot in the plastid. Again, after its quiescence, the exhibition of polarity is lost until either the segmentation of the nucleus or the elongation of the cell wall begins.

ALTERNATION OF GENERATIONS

Since the classical investigations of HOFMEISTER (**20**), it has been universally recognized that the Archegoniatae are characterized by a definite alternation of generations. In this group there are two regularly alternating generations, one bearing sexual reproductive organs and the other producing spores. In sharp contrast to the unanimous agreement in regard to the existence of an alternation of generations in the Archegoniatae, there is a lively contest of contradictory views as to the alternation of generations in the thallophytes. The thallophytes being a loose assemblage of widely diversified types, and investigations on their life histories being far from numerous enough to permit of any generalization, some still question whether a regular alternation of definitely established generations exists in the group, and if it exists, whether it is to be regarded as homologous or antithetic.

Perhaps the first clear statement of a regular alternation of generations in thallophytes is by SACHS (**42**), who endeavored to bring together the facts known in algae and fungi, and to compare them with alternation in the Archegoniatae. SACHS states that the life cycle of algae and fungi is similar to that of the Archegoniatae, one generation producing sexual organs, and the other forming spores. PRINGSHEIM (**36**) held quite a different view, namely that the alternation of generations in the thallophytes consists in the regular succession of a non-sexual or "neutral" generation with a sexual generation, both generations being of similar structure.

Both these views, one by SACHS, who recognized two distinct generations in thallophytes, and the other by PRINGSHEIM, who regarded the two alternating generations as similar structures, have continued to find followers. VINES (**65**) held the view that most of the thallophytes have no alternation of generations, since both sexual and asexual modes of propagation are directly dependent upon the external conditions, and that an alternation of generations in algae comparable to that in the bryophytes is only found in *Coleochaete* and *Chara*. CELAKOVSKY (**5**), although opposing PRINGSHEIM in his conception of alternation of generations in the Archegoniatae, which he designated as the "antithetic," agreed with him in his conception of alternation in thallophytes, in which the successive generations are alike and which conception he designated as the "homologous." PRINGSHEIM'S conception of the homologous alternation of generations in the Archegoniatae has received its principal support in LANG'S experimental cultures (**26**) of the apogamous development of the sporophytes on prothallia of several pteridophytes. CELAKOVSKY'S conception of alternation of generations in the Archegoniatae was taken up fifteen years later by BOWER (**4**), who has supported this conception by his theory of an interpolated sporophytic generation. BOWER holds that the antithetic alternation originated by the intercalation of a non-sexual generation as a new development between two gametophytic generations. This interpolation of a special sporophyte probably took place, according to BOWER, in the algae-like ancestors of the Archegoniatae as they emerged from an aquatic

life to a land life. Moreover, some of the thallophytes, such as *Coleochaete*, Ascomycetes, and Florideae, he holds show the beginning of an antithetic alternation. STRASBURGER (**54**), summarizing cytological results, advanced the theoretical conception of the periodic reduction of chromosomes in the life cycle in plants, thus establishing the view that the x and $2x$ generations which complete the life cycle of the plant are quite distinct from each other. This view has proved the antithetic character of the two generations from a cytological standpoint.

Since that time, cytological investigations of algae which directly touch the problem of the alternation of generations are those of KLEBS (**23**), WILLIAMS (**66**), WOLFE (**70**), LEWIS (**27**), SVEDELIUS (**60**), and of the author (**71, 73, 74, 76**).

KLEBS conducted experimental cultures of several algae, such as *Vaucheria*, *Oedogonium*, and others. By controlling factors such as light, temperature, moisture, oxygen, and chemical composition of nutritive media, he succeeded in producing any kind of reproduction, either sexual or asexual; in other words, he observed no regular alternation of neutral and sexual generations.

WILLIAMS discovered a reduction of chromosomes during the tetraspore formation in *Dictyota*, and this led him to conclude that the tetrasporic plant of *Dictyota* is a sporophytic generation derived from the fertilized egg.

WOLFE showed for *Nemalion* that the cells of the cystocarp have double the number of chromosomes found in the sexual plant, thus presenting the first cytological evidence that the cystocarp of the red algae is sporophytic in character. He placed the period of chromosome reduction at the time of carpospore formation, basing his conclusion on a count of chromosomes in the mitosis just previous to the formation of the carpospores. However, he did not describe the phenomena characteristic of chromosome reduction, namely, the period of synapsis followed by the two divisions which distribute the chromosomes so as to give a numerical reduction.

After the publication of WILLIAMS' and WOLFE'S work, STRASBURGER expressed his agreement with WILLIAMS' conclusion concerning the alternation of generations in the brown algae, but remarked that the tetraspores of the red algae seemed to be different

from those of the Dictyotaceae, and that the place of the chromosome reduction in the red algae should be sought elsewhere than at the formation of tetraspores because some of the red algae develop no tetraspores, but monospores instead. But immediately after the appearance of this view of STRASBURGER, the author's work on *Polysiphonia* was published. He found that the reduction of chromosomes, instead of taking place at the formation of carpospores as reported by WOLFE, occurred at the development of the tetraspores. Thus in the life cycle of *Polysiphonia*, the sporophytic generation is not only represented by cystocarpic branches, but also extends to the tetrasporic plant that alternates antithetically with the sexual plant.

LEWIS then worked out the cytology of *Griffithsia*, special attention being paid to the problem of the alternation of generations. The place of the reduction of chromosomes is in tetraspore formation as in *Polysiphonia*. He concludes that there is in *Griffithsia* as in *Polysiphonia* an antithetic alternation of generations, the gametophytes being represented by the sexual plants and the sporophytes by the sporogenous cells of the cystocarps. In addition to this, there is a regular succession of tetrasporic individuals and sexual individuals; tetrasporic individuals resemble the gametophytes in morphological differentiation and the sporophytes in number of chromosomes. He regards the tetrasporic and sexual plants as presenting homologous alternation.

SVEDELIUS studied the alternation of generations in *Delesseria*. Although his work does not cover the whole life cycle of this type, the cytological studies being made only in the development of tetraspores and vegetative mitosis in both tetrasporic and female plants, yet by comparing his work with that on *Nemalion*, *Polysiphonia*, and *Griffithsia*, he has come to the conclusion that there is an alternation of generations in *Delesseria* as in *Polysiphonia*.

The existence of an alternation of generations in the thallophytes, though somewhat obscure in the green algae on account of insufficient investigations, has been clearly proved by the cytological studies on *Fucus* and *Dictyota* among the brown algae, and on *Nemalion*, *Polysiphonia*, *Griffithsia*, and *Delesseria* among the red algae. Let us now turn to the situation in *Cutleria*.

Since FALKENBERG (12) first suggested that *Cutleria* and *Aglaozonia* may represent the two phases of the life cycle of a single species (*Cutleria*), many workers have tried to secure *Aglaozonia* plants from the cultures of fertilized gametes of *Cutleria*. FALKENBERG and REINKE were the only two who succeeded in producing the form *Falkenbergiana*, an *Aglaozonia* form. The rest of the investigators succeeded in producing either the form *Falkenbergiana* or the form *Churchiana* from unfertilized gametes. Among later workers, SAUVAGEAU, by carrying on his cultures for years, succeeded in getting *Aglaozonia* or *Cutleria* from unfertilized gametes of *Cutleria adspersa*. The conclusion drawn from this result naturally was that the alternation of generations is not necessary, but rather, as it might be called, facultative. OLTMANNS and STRASBURGER have agreed with this view of SAUVAGEAU. The so-called polymorphic character of *Cutleria*, however, needs analytical consideration. The results of the author's investigation are as follows:

The investigation of *Cutleria* plants bearing gametangia showed that the nucleus has 24 chromosomes in both the vegetative and germ cells. The number is doubled at fertilization by the union of the sexual nuclei. The *Cutleria* plant is therefore a gametophyte whose chromosome number is 24. As all now agree, the fertilized gamete or egg with its fusion nucleus should represent the $2x$-generation, and so the fertilized gamete of *Cutleria* is the beginning of the $2x$-generation. The studies of the germination of the fertilized gamete have shown that the $2x$ condition continues in further development. The sporeling developed into a structure unlike the young filamentous form of the parent *Cutleria* as found in nature, but composed of a small upright column and a proportionally large basal disk expansion which became later the dominating region of the further development. Later this expansion develops the zonal structure of *Aglaozonia* as found in nature, and not only resembles *Aglaozonia* in outer morphology, but also in the nuclear conditions, the expansion in cultures and *Aglaozonia* in nature both having 48 chromosomes. *Aglaozonia* in nature produces zoospores, during whose formation 48 chromosomes are reduced to 24, and the zoospores contain 24 chromosomes. The

zoospore with the haploid number germinates with no fusion. The product of the zoosporeling is a filamentous individual like young *Cutleria*, and never produces the zonal flattened form of the parent *Aglaozonia*.

The condition in cultures is very different from the environment in nature. In nature the gametes and zoospores are set free at a depth of 1–5 meters and in cultures they are discharged and kept in sea-water at a depth less than 15–20 cm. Besides, the intensity of light, water-pressure, temperature, and motion of water are also different in these two different environments, and yet the sporelings of the fertilized gametes developed into the flattened disk like young *Aglaozonia* and those of the zoospores grow into filamentous plants like young *Cutleria*. That the potentialities of those two kinds of sporelings in forming invariably the particular individuals different from the parent forms as in nature, even under environmental conditions so different from what is found in nature, and that the potentialities of the two different sporelings have given rise to the particular different individuals, even when they were kept in similar cultures, show that the potential characters of their germ plasm has dominated over the influence of environmental conditions; this dominancy of the innate character over the environmental influence is fundamentally different from the experiments of KLEBS on certain green algae (**23**). Although the two kinds of sporelings from fertilized gametes and zoospores in the cultures have not been kept growing to the stage of reproduction, yet it seems safe enough to infer that the disklike expansion developed from the sporelings of the fertilized gamete will be identical with *Aglaozonia* as found in nature, and the filamentous structures of the zoosporelings will be *Cutleria*. Thus *Cutleria* plants with zoospores represent a gametophytic generation, and *Aglaozonia* plants with fertilized gametes the sporophytic generation. These two generations alternate in the life history of *Cutleria*. The two generations, from the above observations of the cell organization, are fundamentally different and could not be regarded as an example of polymorphism in the sense of OLTMANNS (**35**).

The observations on the sporelings of the unfertilized gametes and studies of their cell organization undoubtedly show that the

female gametes of *Cutleria* are capable of developing into the flattened disk like *Aglaozonia* in nature. Though at first their external morphology presents irregular deviations from forms in nature, the nuclear divisions are perfectly normal. The culture of the sporelings was not continued up to production of reproductive organs, and consequently the discussion cannot be carried on any further. This apogamy may indeed be a reversion to the ancestral type of asexual spores which certainly existed before the appearance of sexuality in the gametophytic generation, but when sexuality is once established, the fusion of gametes and thereby the sporophytic generation is interpolated as a secondary structure in which the reduction of chromosomes occurs.

Summary

The nuclear conditions in the life history of *Cutleria multifida* may be summarized as follows:

1. The nucleus of both male and female plants contains 24 chromosomes, and the male and female gametes contain the same number.

2. In the union of gametes the number is doubled, and 48 chromosomes appear in the sporelings, which develop into the *Aglaozonia* form of *Cutleria*. Therefore, the individual bearing the name of *Cutleria multifida* represents the gametophytic phase of the species, 24 being the gametophytic number of chromosomes; and the *Aglaozonia* form of *Cutleria* represents the sporophytic phase, 48 being the sporophytic number.

3. *Aglaozonia reptans* contains 48 chromosomes, and the number is reduced in zoospore formation, the zoospore containing 24 chromosomes. The zoospore with the reduced number of chromosomes germinates without conjugation. The individual grown from the germinating zoospore presents a striking similarity to the young form of *Cutleria* in nature and contains 24 chromosomes, the same number as the latter. Therefore it is evident that the individual bearing the name of *Aglaozonia reptans* represents the sporophytic phase of the species, 48 being the sporophytic number of chromosomes, and that the gametophytic phase is represented

by the individual grown from the zoospore and resembling the young form of *Cutleria* in nature. It is certain that *Aglaozonia reptans* as it occurs in nature is identical with the *Aglaozonia* form of *Cutleria multifida* as developed in cultures and now determined to be the sporophytic phase of the species.

4. Therefore, *Cutleria multifida* and *Aglaozonia reptans* represent respectively gametophytic and sporophytic generations of a single species, the two generations alternating in the life history of *Cutleria*.

5. The female gamete of *Cutleria* may germinate apogamously. There is no irregularity in the mitotic process, 24 chromosomes being invariably present. The individual produced, in its early development differs somewhat from the product of the fertilized gamete, but the fate of the apogamous individual was not determined.

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EXPLANATION OF PLATES XXVI–XXXV

All figures were drawn with the aid of a camera lucida under the Zeiss apochromatic objective 1.5 mm. N.A. 130, in combination with compensating ocular 12; except figs. 200–202, which were drawn with compensating ocular 18; figs. 8, 9, 14, drawn with compensating ocular 8; and figs. 1–7, 12, 13, 16, 17, 53, 144–150, drawn with ocular 4; and figs. 10, 11, 15, which were drawn under Zeiss apochromatic objective 16 mm. combined with compensating ocular 12. The figures are reduced to one-half the original size. Figs. 1–15 are in the text.

PLATE XXVI

The formation of the male gametangium of Cutleria multifida

Fig. 16.—Portion of the thallus of a male plant, showing a single layer of superficial cells and the larger cells below.

Fig. 17.—Portion of the thallus of a male plant, where 4 superficial cells have grown into papillae, the male gametangium initials.

Fig. 18.—Male gametangium initial: nucleus in resting condition.

Fig. 19.—Prophase of nucleus: 24 chromosomes and a nucleolus present.

Fig. 20.—Metaphase: the nuclear cavity in this stage strikingly diminished.

Fig. 21.—A filament with two male gametangia: nucleus in the young gametangium initial at metaphase.

Fig. 22.—Anaphase that follows the metaphase of fig. 20.

Fig. 23.—Nucleus already divided and each daughter nucleus now in prophase; 24 chromosomes present in each.

Fig. 24.—Nucleus in the lower cell in advanced prophase, while the nucleus in the upper cell is still in early prophase.

FIG. 25.—Similar stage to fig. 24, excepting the presence of centrosome-like structures at the poles.

FIG. 26.—Nucleus in the lower cell in anaphase; nucleus in the upper cell in resting condition.

FIG. 27.—Metaphase of the nucleus in the upper cell of 2-celled stage; the lower cell is not drawn.

FIG. 28.—Late metaphase of the nucleus in the upper cell; nucleus in the lower cell in resting condition.

FIG. 29.—Telophase of nucleus of the upper cell; a new cell wall is being laid down between two daughter nuclei.

FIG. 30.—Male gametangium of 3 cells: the nuclei in the upper two cells are in resting condition; the nucleus in the basal cell in prophase, showing 24 chromosomes and a nucleolus.

FIG. 31.—Male gametangium of 3 cells: the nucleus in the terminal cell is in metaphase; centrosome-like structures at the poles of the spindle.

FIG. 32.—Male gametangium of 3 cells: the nucleus in the terminal cell in metaphase, with centrosome-like structures at the poles; the nucleus in the middle cell in anaphase, and that of the basal cell in resting stage.

FIG. 33.—Male gametangium of 4 cells: the nucleus in the terminal cell is in metaphase; that of the middle cell in prophase, showing 24 chromosomes.

FIG. 34.—Male gametangium of 4 cells: two nuclei are in prophase; 24 chromosomes are clearly present; one in anaphase and the other in resting condition.

FIGS. 35, 36.—Mitotic figures of the nucleus in a vegetative filament: fig. 35, anaphase; fig. 36, prophase, showing 24 chromosomes.

FIGS. 37, 38.—Cross-section of a male gametangium of 5 cells: fig. 37, metaphase of the mitosis which divides the filament into two rows of cells; fig. 38, prophase of the same, showing 24 chromosomes.

FIG. 39.—Tip of a vegetative filament, showing stages in the formation of male gametangia; the male gametangia have arisen from the third, fourth, sixth, and seventh cells; four nuclei in the three young gametangia are in prophase; 24 chromosomes can be counted in each.

FIG. 40.—Portion of a male gametangium of 2 rows of cells: one nucleus in metaphase, one in prophase showing 24 chromosomes, and three others in the resting condition.

FIG. 41.—Portion of a more advanced male gametangium: four nuclei in prophase, clearly showing the 24 chromosomes.

FIG. 42.—Cross-section of a male gametangium at about the same stage as in fig. 41; one nucleus is in prophase; 24 chromosomes present.

FIG. 43.—Portion of a male gametangium at about the same stage as in fig. 41; two nuclei are in anaphase.

FIG. 44.—Cross-section of a male gametangium at about the same stage as in fig. 43: two nuclei in prophase of the mitosis which divides the filament into a structure with four rows of cells.

FIG. 45.—Portion of a male gametangium consisting of 4 rows of cells: one nucleus is in anaphase.

FIG. 46.—Portion of a male gametangium at about the same stage as in fig. 45: one nucleus is in prophase, showing clearly 24 chromosomes.

FIGS. 47, 48.—Portion of a male gametangium at a more advanced stage: one nucleus in fig. 47 in prophase, showing 24 chromosomes; one nucleus both in figs. 47 and 48 in metaphase; and two nuclei in fig. 48 in anaphase.

FIG. 49.—Portion of a male gametangium, showing the last division of nuclei; one nucleus is in prophase and the other in metaphase.

FIG. 50.—Cross-section of a male gametangium at about the same stage as in fig. 49; one nucleus is in prophase, two others in metaphase of the mitosis which divides the filament into a structure of 8 rows of cells.

FIG. 51.—Cross-section of a mature male gametangium: nuclei are in resting condition.

FIG. 52.—Cross-section of a mature male gametangium, showing the plastids that are associated with the red pigment.

PLATE XXVII

The formation of the female gametangium of Cutleria multifida

FIG. 53.—Portion of thallus of a female plant, showing a single layer of superficial cells and the larger cells below; one of the superficial cells has increased in size, and will be the female gametangium later.

FIG. 54.—One of the superficial cells becomes still larger in size: nucleus is in prophase; 24 chromosomes and a nucleolus are present.

FIG. 55.—Nucleus in metaphase; centrosome-like structures at the poles of spindle.

FIG. 56.—Anaphase.

FIG. 57.—Later telophase: cell wall is being laid down between the newly formed daughter nuclei.

FIG. 58.—Female gametangium of 2 cells.

FIG. 59.—Nucleus of the upper cell in prophase; nucleus of the basal cell in resting condition.

FIG. 60.—Nucleus of upper cell in metaphase.

FIG. 61.—Nucleus of upper cell in anaphase.

FIG. 62.—Late telophase of nucleus in upper cell.

FIG. 63.—Female gametangium consisting of 2 cells: nucleus of basal cell in metaphase.

FIG. 64.—Nucleus in basal cell in anaphase.

FIG. 65.—Female gametangium of 3 cells: nucleus of basal cell in prophase; 24 chromosomes and a nucleolus are present.

FIG. 66.—Nucleus of terminal cell in prophase, showing 24 chromosomes; nucleus of basal cell in metaphase.

FIG. 67.—Nucleus of terminal cell in metaphase.

FIG. 68.—Nucleus of terminal cell in anaphase.

FIG. 69.—Nucleus of middle cell in prophase.

FIG. 70.—Nucleus of middle cell in early anaphase.

FIG. 71.—Cross-section of a female gametangium of 2 cells: nucleus in anaphase viewed from the pole, clearly showing 24 chromosomes.

FIG. 72.—Cross-section of a female gametangium of 5 cells: nucleus in metaphase of the mitosis which divides the gametangium into a structure composed of 2 rows of cells.

PLATE XXVIII

The formation of the female gametangium of Cutleria multifida (continued)

FIG. 73.—Cross-section of a female gametangium of 8 cells in two rows: one nucleus in late prophase, showing 24 chromosomes.

FIG. 74.—Portion of a female gametangium of 8 cells in two rows: one nucleus in late prophase, polar view of which is shown in the previous figure; nucleus in basal cell in early prophase.

FIG. 75.—Portion of a female gametangium of 7 cells: one nucleus is in late prophase, showing 24 chromosomes, which will result in two cells arranged side by side in the direction perpendicular to the plane of the paper.

FIG. 76.—Portion of a female gametangium of 8 cells: one nucleus in anaphase.

FIG. 77.—Portion of a female gametangium of 8 cells: one nucleus in late anaphase.

FIG. 78.—Cross-section of a female gametangium of 10 cells: one nucleus in metaphase of the division which divides the gametangium into a structure of three rows of cells.

FIG. 79.—Portion of a female gametangium of 10 cells: one nucleus in metaphase.

FIGS. 80, 81.—Portion of a female gametangium of 10 cells: one nucleus in anaphase in both figures.

FIG. 82.—Portion of a female gametangium of 10 cells: one nucleus is in metaphase and two others have already divided.

FIG. 83.—Portion of a female gametangium of 10 cells: one nucleus in prophase, showing 24 chromosomes, one nucleus in late anaphase and the other two have already divided.

FIG. 84.—Portion of a female gametangium of 10 cells: one nucleus in early metaphase viewed from the pole, showing 24 chromosomes.

FIG. 85.—Portion of a female gametangium of 12 cells: one nucleus in anaphase and the other two have already divided.

FIG. 86.—Portion of a female gametangium of 12 cells: one nucleus in early metaphase, viewed from the pole, showing 24 chromosomes; the other nucleus in metaphase in lateral view.

FIG. 87.—Portion of a female gametangium of 15 cells: one nucleus in prophase.

FIG. 87*a*.—The nucleus in prophase in the previous figure under higher magnification: 24 chromosomes present.

FIGS. 88, 88*a*.—Portion of a female gametangium of 18 cells: one nucleus in anaphase, which is shown under higher magnification in fig. 88*a*.

FIG. 89.—Cross-section of mature female gametangium in 4 tiers.

FIG. 90.—Cross-section of mature female gametangium in 8 tiers.

FIG. 91.—Two cells of a mature female gametangium: the plastids and dense cytoplasm are thick along the inner wall; nuclei in resting condition.

FIG. 92.—One cell of a mature female gametangium: plastids and cytoplasm are thick toward the outer wall; nucleus in resting condition.

FIG. 93.—A female gametangium entirely emptied after the escape of female gametes.

PLATE XXIX

The union of gametes and germination of the fertilized female gamete

FIG. 94.—Two male gametes which have stopped the swimming movement; cilia are withdrawn, nuclear membranes are scarcely visible, and the reticulum shows 24 chromosomes.

FIG. 95.—Union of male and female gametes: nucleus of the male gamete shows 24 chromosomes and that of the female gamete is in the resting condition; no cell membrane is recognizable around the gametes.

FIG. 96.—Cytoplasm of male gamete is entirely fused with that of female gamete and the whole body of the united gametes has about assumed the spherical form; cell membrane has appeared; male nucleus still shows 24 chromosomes.

FIG. 97.—Male nucleus has advanced toward the female nucleus.

FIG. 98.—Male nucleus has moved nearer toward the female nucleus.

FIG. 99.—Male nucleus is attached to the female nucleus.

FIG. 100.—Male nucleus, showing 24 chromosomes, and female nucleus in resting condition.

FIG. 101.—Male nucleus very closely applied to the female nucleus; 24 chromosomes of the male nucleus still recognizable; a part of the cell wall of the sporeling has thickened.

FIG. 102.—Part of the male nucleus, evidently consisting exclusively of chromosomes, has become submerged in the female nucleus, which is in the resting condition.

FIG. 103.—Male nucleus has completely entered into the female nucleus; dense chromatin granules are to be seen at the part of female nucleus where the male nucleus has entered.

FIG. 104.—Fusion nucleus: network contains a number of chromatin granules that show no distinction between those derived from the male and female nuclei.

FIG. 105.—Fusion nucleus is in the resting condition.

FIG. 106.—Prophase: 48 chromosomes and a nucleolus are present; the chromosomes are apparently alike both in form and size; the sporeling shows an elongation at a point where the cell wall is thickened.

FIG. 107.—Metaphase: thickening of cell wall is present, though the elongation of the sporeling has not yet begun.

FIG. 108.—Fusion nucleus in very early prophase: characteristic elongation of the sporeling and thickening of the corresponding cell wall at that part is remarkable.

FIG. 109.—Portion of the elongated part of a sporeling with a resting nucleus.

FIG. 110.—Cross-section of the elongated portion of a sporeling at the same stage as the previous figure; fusion nucleus in prophase; 48 chromosomes are present.

FIG. 111, *a*, *b*.—Two sections of a sporeling: nucleus in prophase, showing 48 chromosomes; elongation and correponding thickening of the cell wall are evident.

FIG. 112.—Metaphase: Elongation of the sporeling and thickening of the cell wall at the point of the elongation are marked; axis of the figure is in the direction of the elongation.

FIG. 113.—Cross-section of a sporeling perpendicular to the axis of elongation; nucleus in late metaphase.

FIG. 114.—Cross-section of a sporeling at about same stage as in fig. 112; nucleus in metaphase is seen from the pole; 48 chromosomes are present.

FIG. 115.—Sporeling in 2-celled stage: two nuclei in resting condition.

FIG. 116.—Sporeling in 2-celled stage: nucleus in terminal cell in prophase, and that of basal cell in resting condition.

FIG. 117.—Sporeling in 2-celled stage: nucleus in terminal cell very small and in resting condition, while that of basal cell shows very early prophase.

FIG. 118.—Cross-section through a basal cell of a sporeling in 2-celled stage: nucleus is in late prophase; 48 chromosomes present.

FIG. 119.—Sporeling in 2-celled stage: nucleus in terminal cell in early prophase, and that of basal cell in resting condition.

FIG. 120.—Sporeling in 2-celled stage: nucleus in terminal cell in prophase, showing 48 chromosomes.

FIG. 121.—Sporeling in 3-celled stage: nucleus in basal cell in prophase, showing 48 chromosomes.

FIG. 122.—Sporeling in 3-celled stage: nucleus in basal cell in metaphase.

FIG. 123.—Sporeling in 3-celled stage: all the nuclei in prophase, showing 48 chromosomes.

PLATE XXX

The germination of the unfertilized female gamete

FIG. 124.—A female gamete in the resting condition: cell wall does not seem to be developed excepting at the point where a slight elongation is noticeable.

FIG. 125.—Cell wall is now recognizable, especially at the elongated point; nucleus in resting condition.

FIG. 126.—Nucleus with 24 chromosomes is prophase.

FIG. 127.—Nucleus in metaphase: contour of sporeling almost spherical.

FIG. 128.—Polar view of same stage as in previous figure: 24 chromosomes.

FIG. 129.—Polar view of metaphase showing 24 chromosomes: characteristic elongation and the thickened cell wall of the elongated part are recognizable.

FIG. 130.—Metaphase of same stage as in previous figure: axis of the figure is perpendicular to that of the previous one.

FIG. 131.—Anaphase.

FIG. 132.—Metaphase of the similar stage as in figure 130, but axis of the figure is perpendicular to that.

FIG. 133.—Anaphase.

FIG. 134.—Late telophase: elongation of the sporeling is remarkable.

FIG. 135.—Sporeling of 2-celled stage: nuclei in resting condition.

FIG. 136.—Sporeling of 2-celled stage: nucleus of terminal cell in prophase; 24 chromosomes present.

FIG. 137.—Sporeling of 2-celled stage: nucleus of terminal cell in metaphase viewed from pole; nucleus of basal cell in prophase; 24 chromosomes present.

FIG. 138.—Sporeling of 2-celled stage: nucleus of terminal cell in prophase; form of the chromosomes is rather long.

FIG. 139.—Sporeling of 2-celled stage: nucleus in basal cell in anaphase.

FIG. 140.—Sporeling of 2-celled stage: nucleus in terminal cell in late telophase and that of basal cell in metaphase, showing 24 chromosomes in polar view.

FIG. 141.—Sporeling in 3-celled stage: nucleus of basal cell in prophase, showing 24 chromosomes.

FIG. 142.—Sporeling in 3-celled stage: nucleus of middle cell in prophase, showing 24 chromosomes.

FIG. 143.—Sporeling in 3-celled stage: nucleus of basal cell in metaphase.

FIG. 144.—Sporeling of 12-celled stage.

FIG. 145.—Sporeling of 13-celled stage.

FIG. 146.—Sporeling of 22-celled stage.

PLATE XXXI

The formation of the zoosporangium of Aglaozonia reptans

FIG. 147.—Portion of a young thallus, showing a single layer of superficial cells and the larger cells below.

FIG. 148.—Portion of a young thallus, showing a single layer of superficial cells, hypodermal cells, and the larger cells below.

FIG. 149.—Portion of thallus in more advanced stage.

FIG. 150.—Portion of thallus in still more advanced stage: superficial cells have grown in size and will be zoosporangia or zoospore mother cells.

FIG. 151.—Young zoospore mother cell and stalk cell.

FIG. 152.—Zoospore mother cell of characteristic club-shape; nucleus in resting condition.

FIG. 153.—Resting nucleus slightly increased in size.

FIG. 154.—Resting nucleus with radiations at one pole.

FIG. 155.—Section of a mother cell cut obliquely: resting nucleus with radiations at two poles.

FIG. 156.—Nucleus in very early prophase, situated at one side, with a centrosome-like structure but no radiations.

FIG. 157.—Nucleus situated at the upper part of the mother cell with two centrosome-like structures and radiations.

FIG. 158.—Nucleus situated at the upper part with a centrosome-like structure and radiations.

FIG. 159.—Nucleus situated at the middle part with no radiations.

PLATE XXXII

The formation of the zoosporangium of Aglaozonia reptans (continued)

FIG. 160.—Nucleus of a zoospore mother cell in prophase, chromatin network irregularly traversing the nuclear cavity.

FIGS. 161–168.—Nucleus in synapsis.

FIG. 161.—Chromatin threads have begun to be arranged in form of loops which become attached by their ends to a part of the nuclear membrane.

FIG. 162.—Formation of loops is further advanced.

FIG. 163.—Cross-section of a mother cell; attachment of loops is at the side.

FIG. 164.—Attachment of loops to the nuclear membrane is all the way around.

FIG. 165.—Some of the loops are quite shortened and thickened, and yet some others are left behind and can be recognized running across the cavity.

FIG. 166.—Section near the base of crowded loops in contact with the membrane, showing 48 or more isolated cut sections of the loops.

FIG. 167.—Loops have shortened and thickened.

FIG. 168.—Nucleus emerging from synapsis: two pairs of chromatin loops are already in the form of chromosomes.

FIG. 169.—Majority of the two arms of each of these loops are going to form paired arms of bivalent chromosomes.

FIG. 170.—Diakinesis stage: 24 bivalent chromosomes are present; no polar radiations.

FIG. 171.—Spindle with two poles has just formed.

FIG. 172.—Metaphase.

FIG. 173.—Polar view of the metaphase, showing 24 bivalent chromosomes at the equatorial plate.

PLATE XXXIII

The formation of the zoosporangium of Aglaozonia reptans (continued)

As the stage advances, gradual increase of the thickening of the cell wall at the tip of the mother cell is noticeable.

FIG. 174.—Late metaphase.

FIG. 175.—Anaphase: 24 chromosomes at each pole.

FIG. 176.—Anaphase, side view.

FIG. 177.—Anaphase, further advanced.

FIG. 178.—Telophase.

FIG. 179.—Later telophase: two daughter nuclei in resting condition.

FIG. 180.—Two daughter nuclei increased in size: each nucleus has radiations at the poles.

FIG. 181.—Upper nucleus has grown considerably larger than the lower one.

FIG. 182.—Two nuclei are in contact.

FIG. 183.—Upper nucleus is in prophase; lower one still in resting condition.

FIG. 184.—Two nuclei simultaneously in metaphase.

FIG. 185.—Anaphase.

FIG. 186.—Late anaphase: a group of chromosomes at one pole of the upper nucleus is not indicated in this figure.

PLATE XXXIV

The formation of the zoosporangium of Aglaozonia reptans (continued)

FIG. 187.—Telophase of the second division in the mother cell.

FIG. 188.—Late telophase.

FIG. 189.—Metaphase of the third division.

FIG. 190.—Telophase of the same: 8 nuclei present.

FIGS. 191–193.—Zoospore mother cells drawn from unstained preparations.

FIG. 191.—Nucleus in prophase: numerous granules of various sizes are recognizable; globular structures of larger size are plastids.

FIG. 192.—Four-nucleate stage: numerous granules still visible; plastids have increased in number.

FIG. 193.—Eight-nucleate stage: plastids have much increased in number and the thickness of the cell wall at the top of the mother cell is noticeable.

FIG. 194.—Cross-section of a mother cell at about same stage as in fig. 190; plastids mostly arranged near the cell membrane.

FIG. 195.—Portion of a mother cell near maturity: thickness of the cell wall at the top of the mother cell has increased; plastids moving toward the nuclei and surrounding them.

FIG. 196.—Later stage: plastids are around the nuclei.

FIG. 197.—Portion of a mother cell: cytoplasm has become detached from the cell wall and cleavage furrows have appeared, so that general outlines of individual zoospores are established.

FIGS. 198, 199.—Portion of a mother cell containing zoospores.

FIG. 200.—Portion of cell wall at the tip of a mother cell after maturity: the cell wall in this part is considerably thickened and swollen.

FIG. 201.—Later stage: the cell wall at the tip of the mother cell has disintegrated into two lamellae.

FIG. 202.—Further advanced stage approaching the discharge of zoospores: disintegration has still progressed and broken the cell wall into three lamellae.

PLATE XXXV

The germination of the zoospore of Aglaozonia reptans

FIG. 203.—Zoospore 2 hours after becoming quiescent: cell wall has just developed; resting nucleus with a centrosome-like structure and radiations.

FIG. 204.—Zoospore 20 hours after becoming quiescent: nuclear condition is about similar to fig. 203.

FIG. 205.—Zoospore 24 hours after becoming quiescent: no radiations visible.

FIGS. 206–208.—Drawn from material fixed 24 hours after becoming quiescent.

FIG. 206.—Resting nucleus with radiations: elongation of the sporeling and thickening of cell wall at the elongated part is noticeable.

FIG. 207.—About the same stage as in the previous figure.

FIG. 208.—Early prophase.

FIG. 209.—Prophase: 24 chromosomes clearly present.

FIG. 210.—Cross-section through the elongated part of a sporeling: nucleus in prophase, showing 24 chromosomes and a nucleolus.

FIG. 211.—Metaphase: general contour of the sporeling is spherical.

FIG. 212.—Polar view of the metaphase; 24 chromosomes clearly in view.

FIG. 213.—Metaphase: the sporeling has elongated.

FIG. 214.—Metaphase viewed from the pole: the sporeling has elongated at two points.

FIG. 215.—Anaphase.

FIG. 216.—Telophase.

FIG. 217.—Sporeling of 2 cells: nucleus of the basal cell is in prophase; 24 chromosomes visible.

FIG. 218.—Sporeling of 2 cells: nucleus in metaphase.

FIG. 219.—Sporeling of 2 cells: nucleus of terminal cell in early prophase; 24 chromosomes present.

FIG. 220.—Nucleus of terminal cell in prophase.

FIG. 221.—Nucleus of terminal cell in metaphase viewed from pole.

FIG. 222.—Two nuclei simultaneously in prophase; 24 chromosomes present.

FIG. 223.—Sporeling of 3 cells.

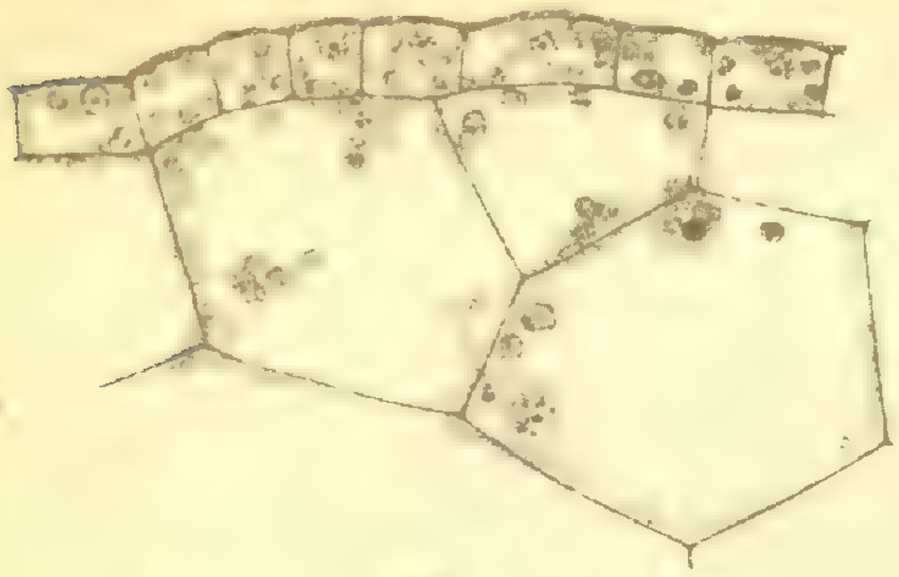
FIG. 224.—Sporeling of 3 cells: nucleus in middle cell in prophase; 24 chromosomes present.

FIG. 225.—Sporeling of 3 cells: nucleus in basal cell in prophase; 24 chromosomes present.

FIG. 226.—Sporeling of 4 cells.

FIG. 227.—Sporeling of 4 cells: nuclei in lower cells in metaphase.

FIG. 228.—Sporeling of 4 cells: two upper cells lie side by side in the direction perpendicular to the axis of the sporeling.



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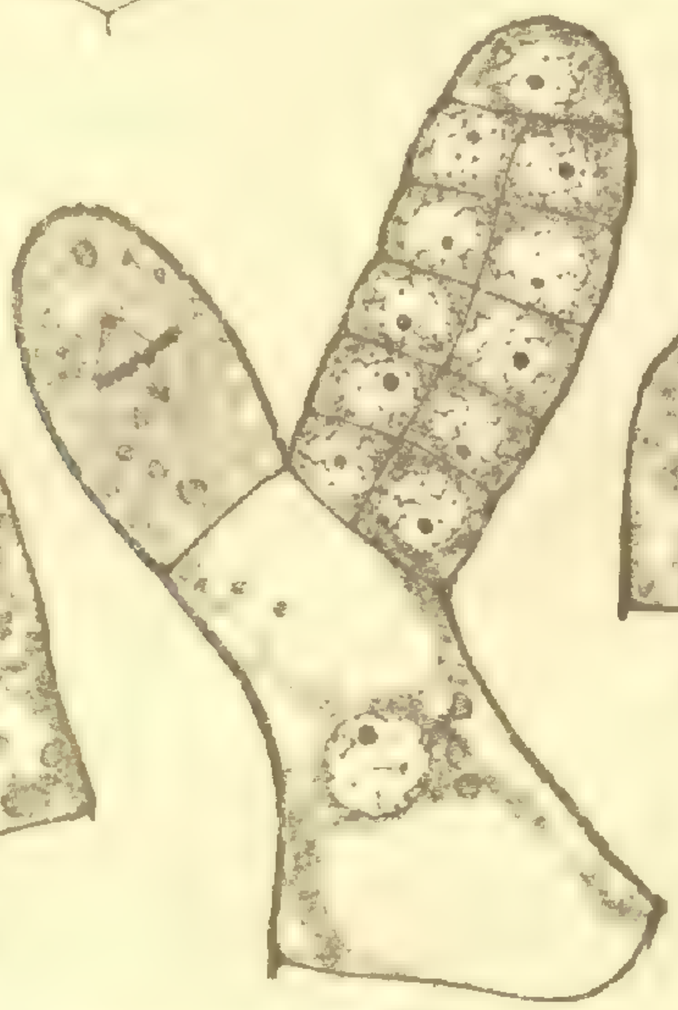

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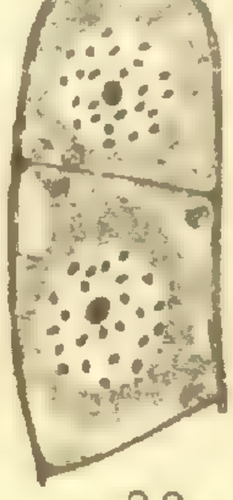

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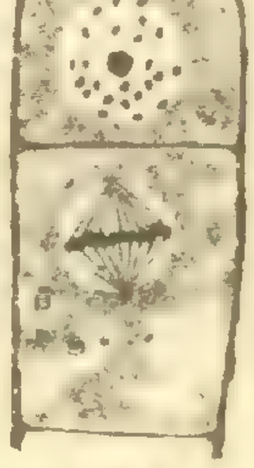

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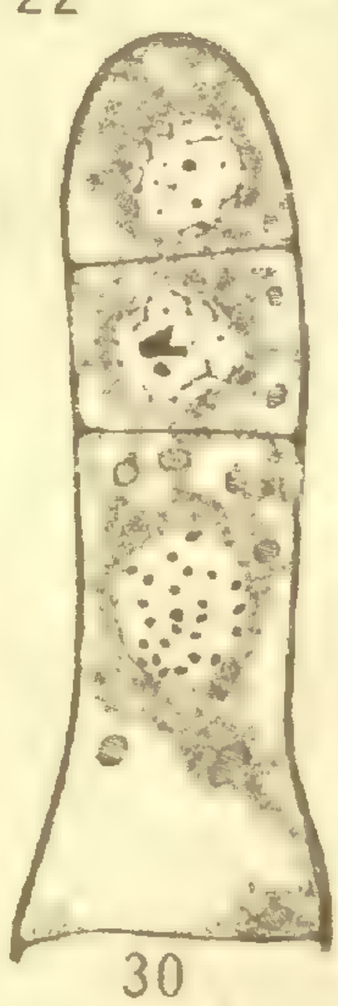

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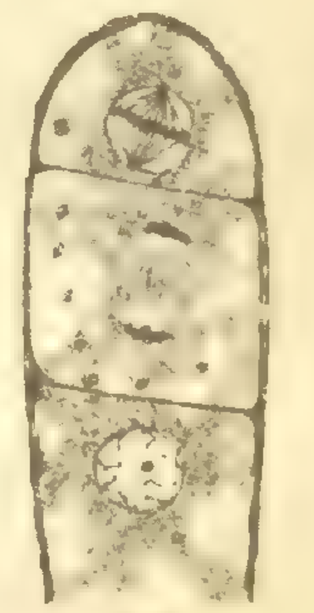

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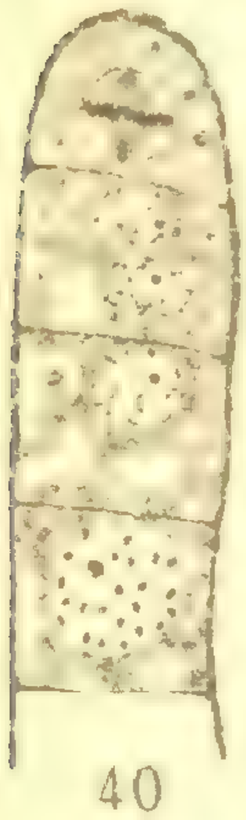

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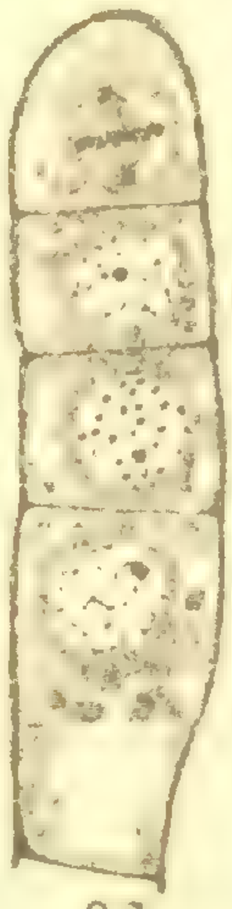

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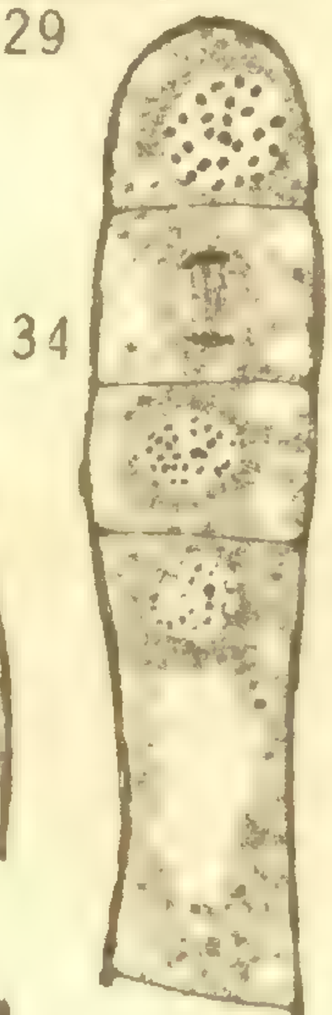

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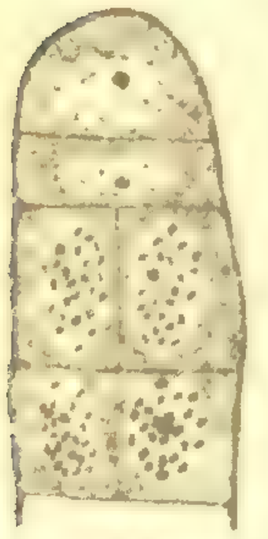

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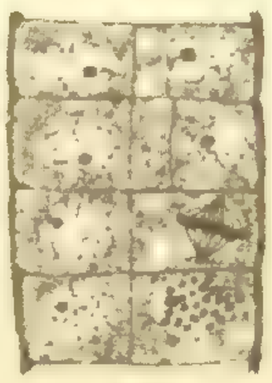

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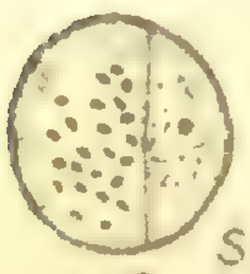

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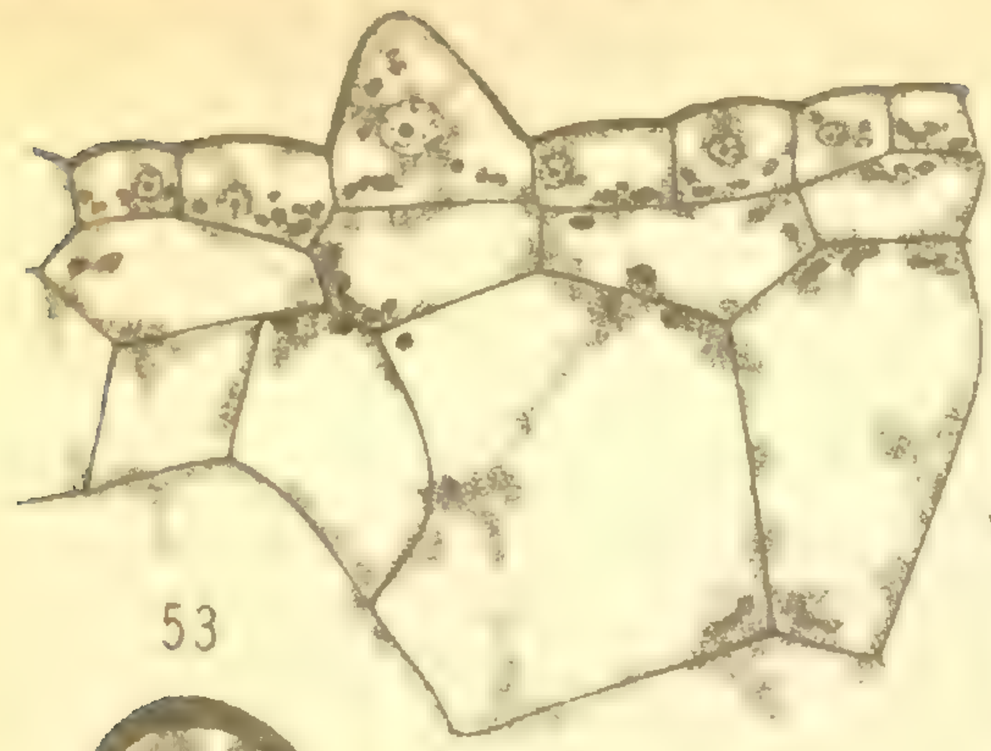
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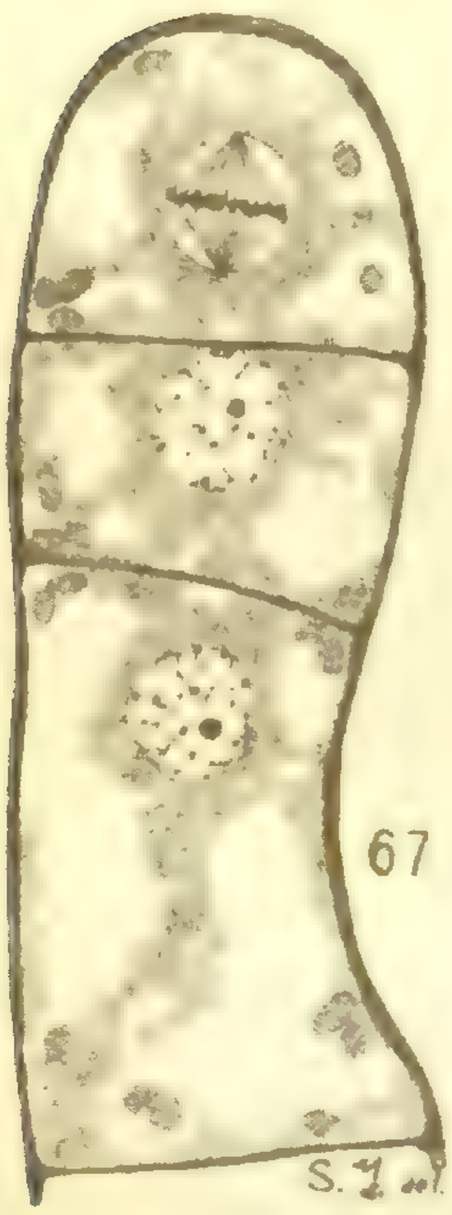
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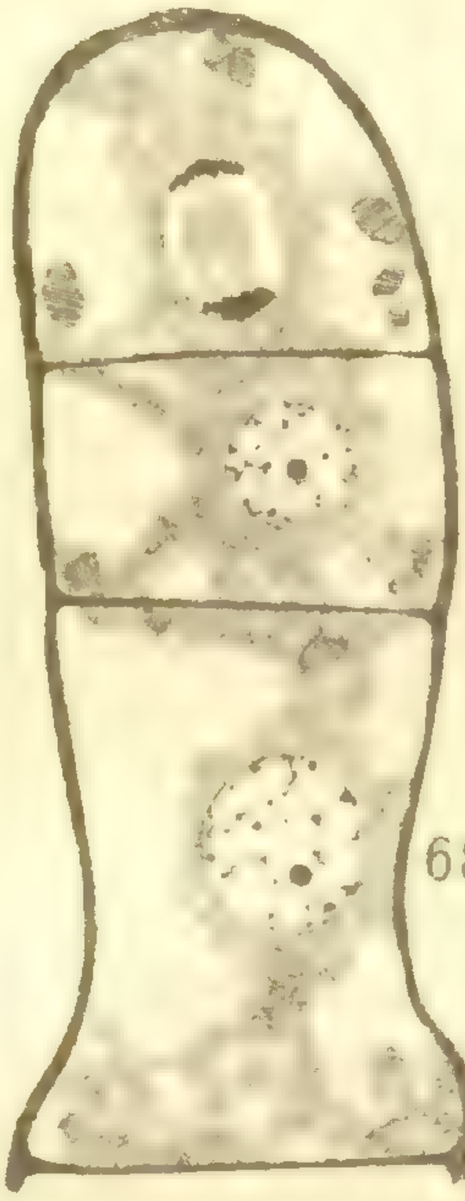
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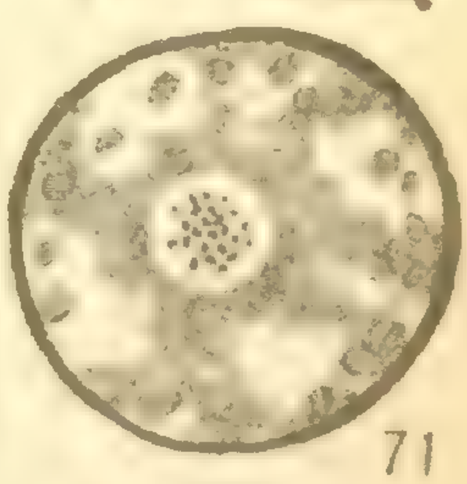
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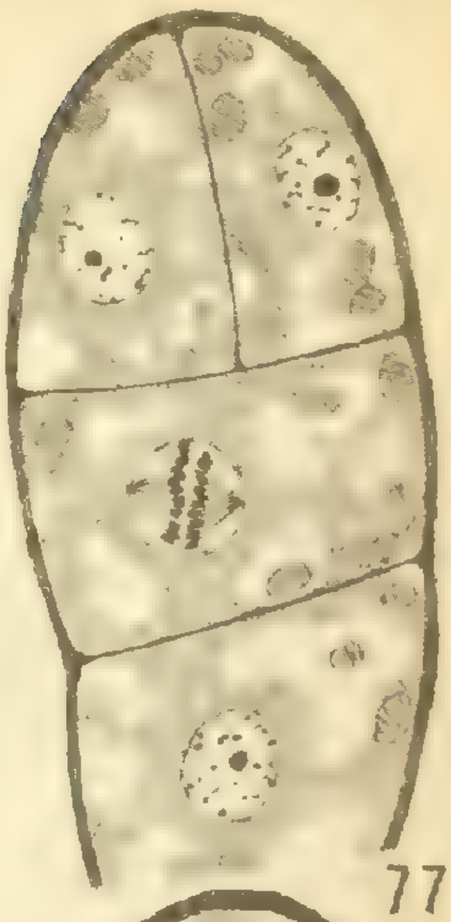
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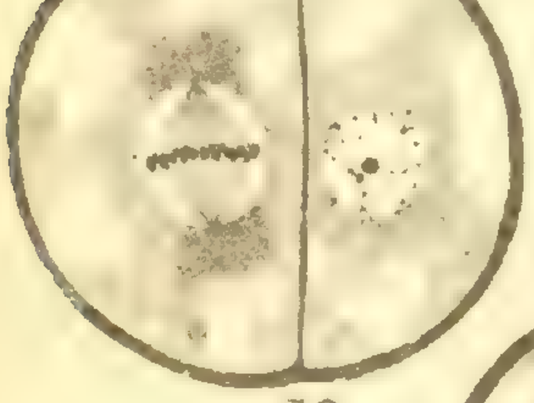
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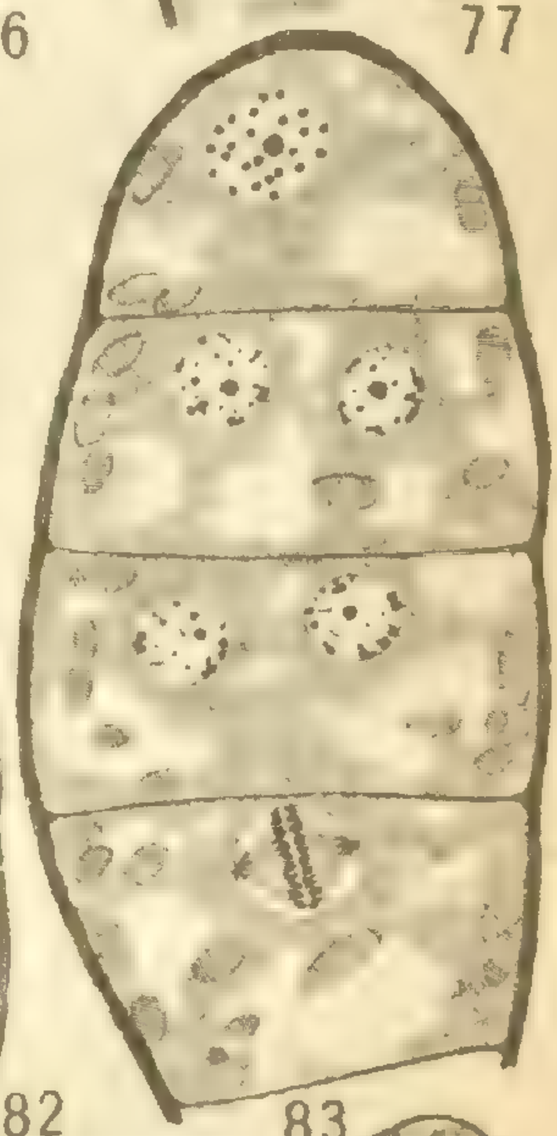
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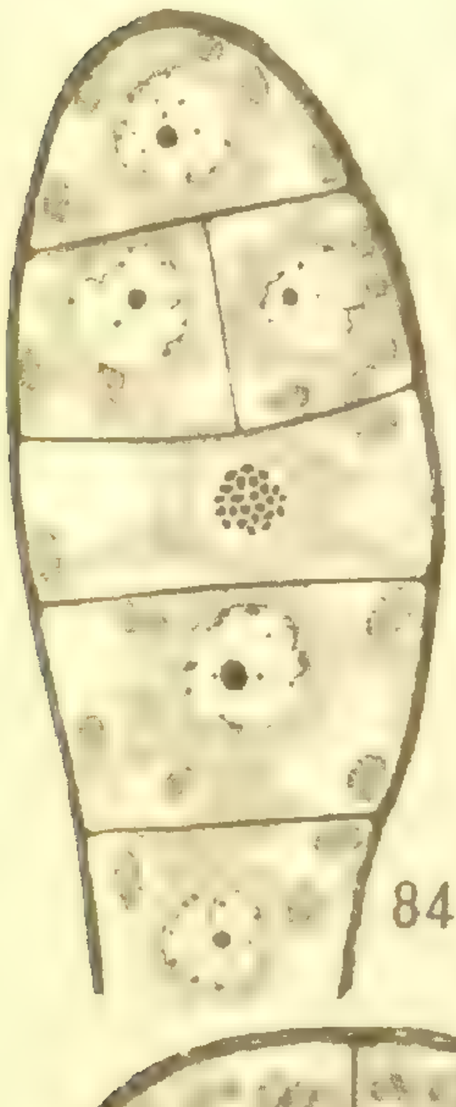
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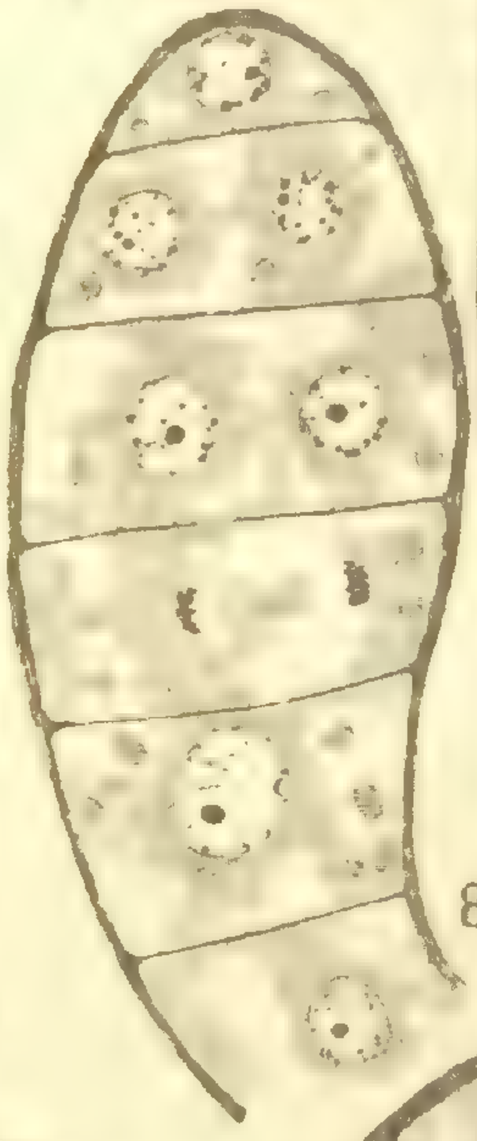
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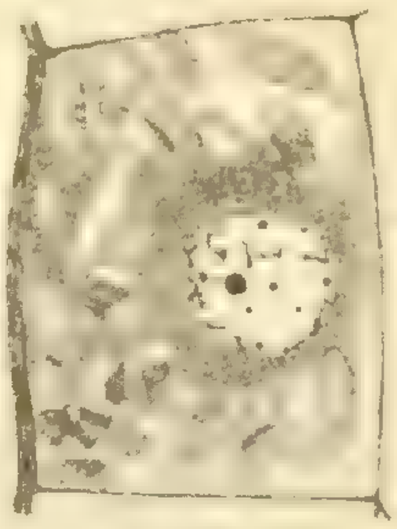
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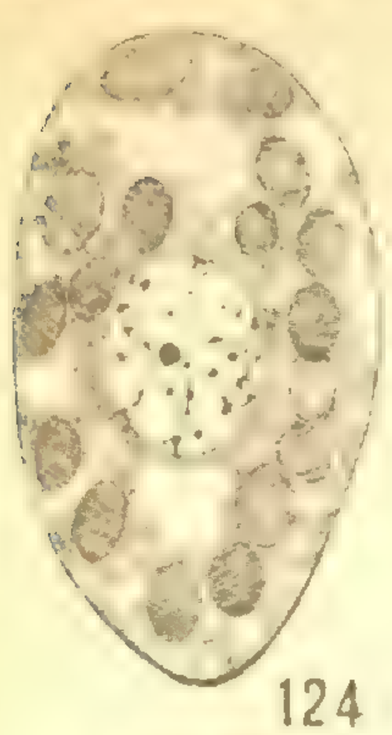
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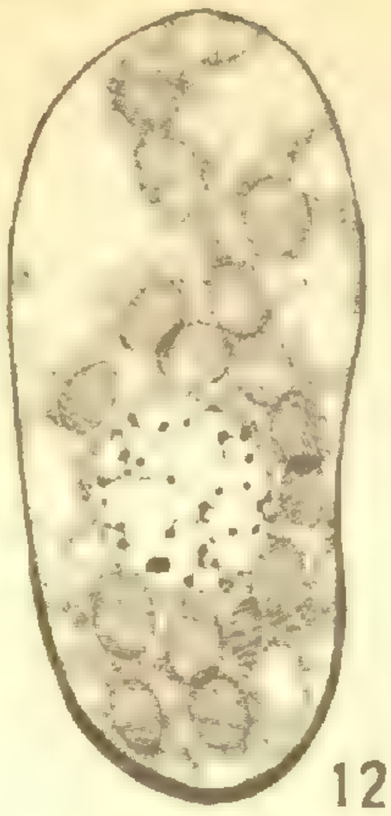
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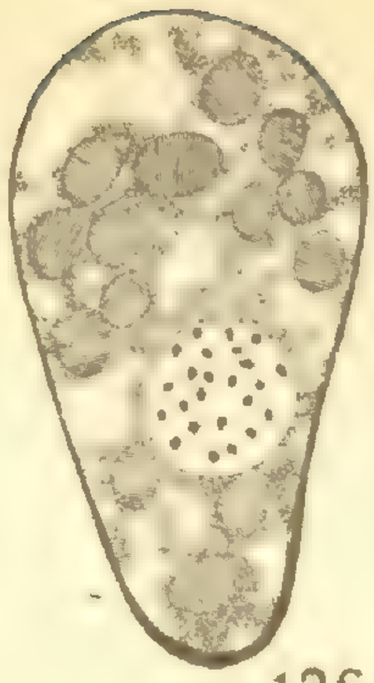
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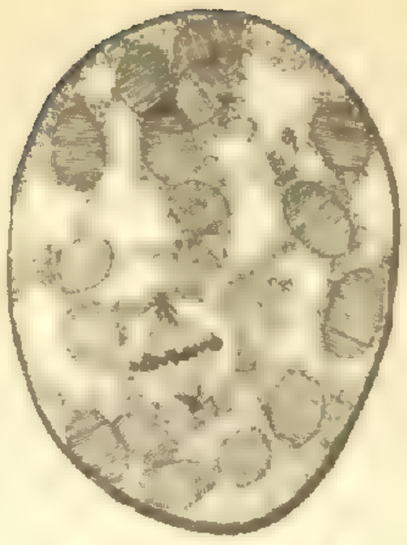
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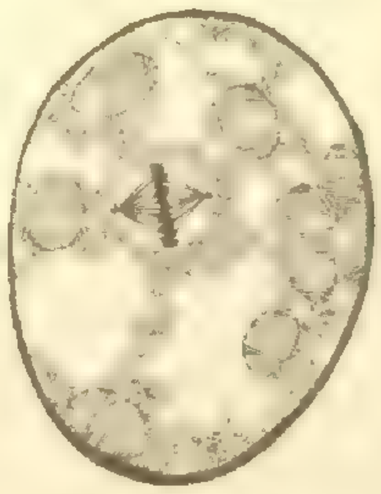
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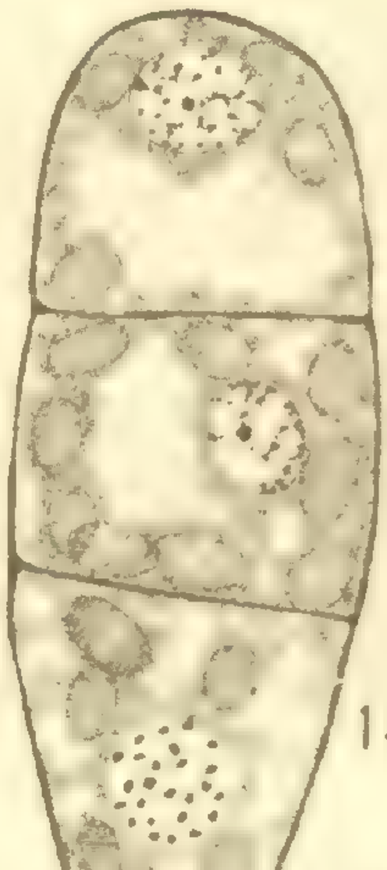
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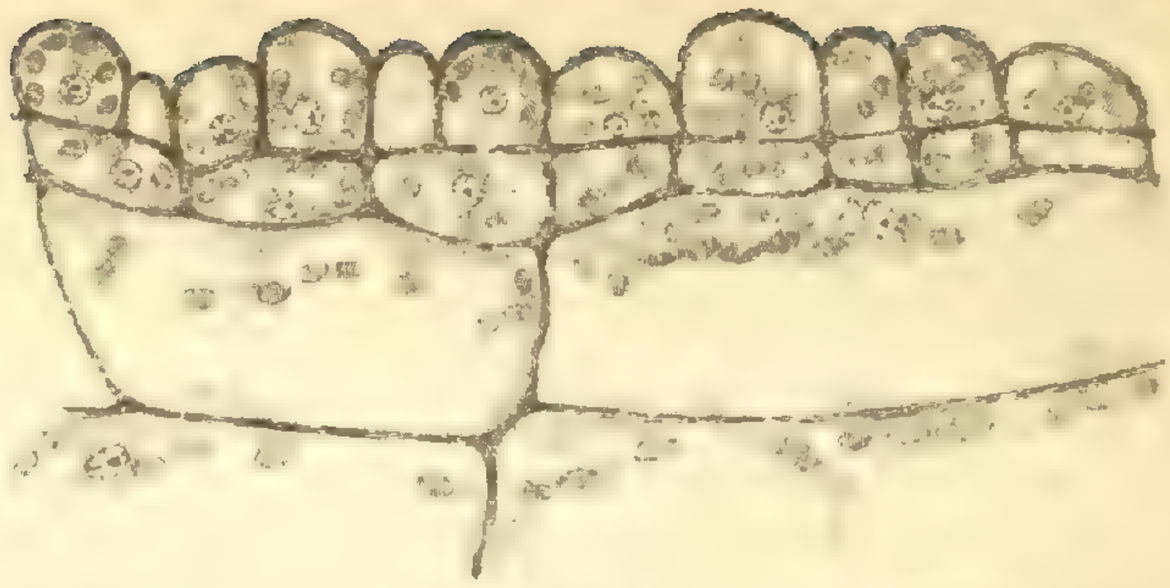

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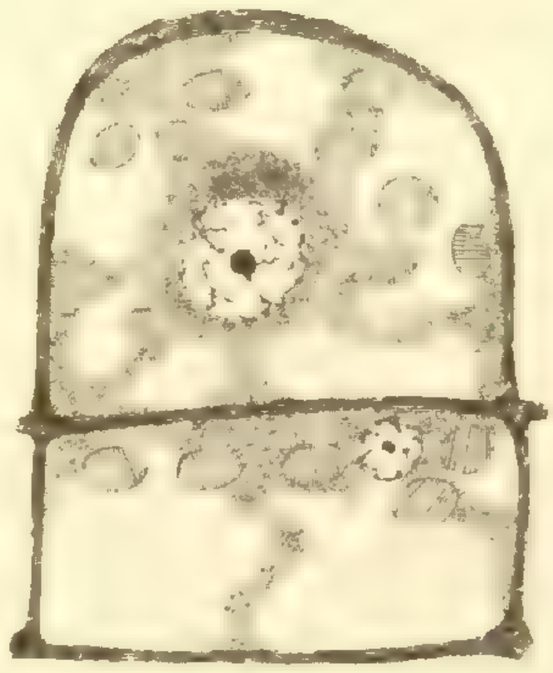

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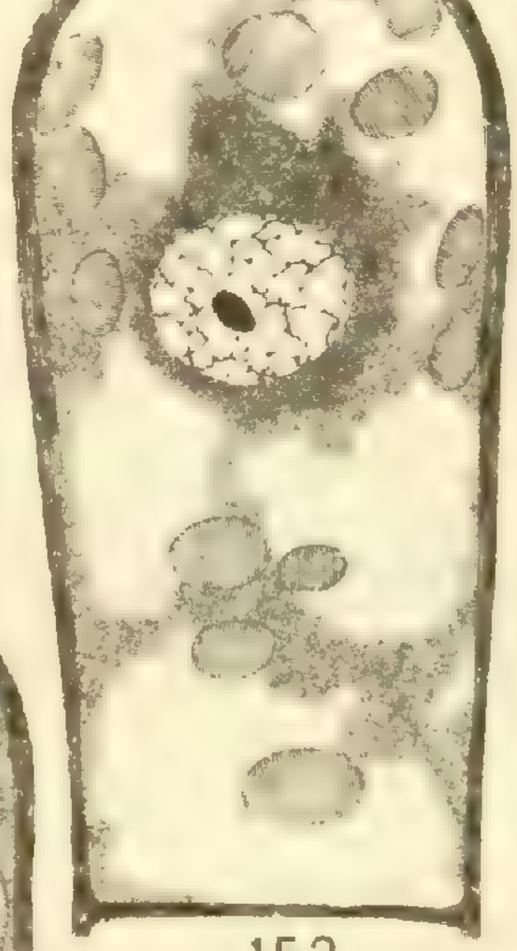

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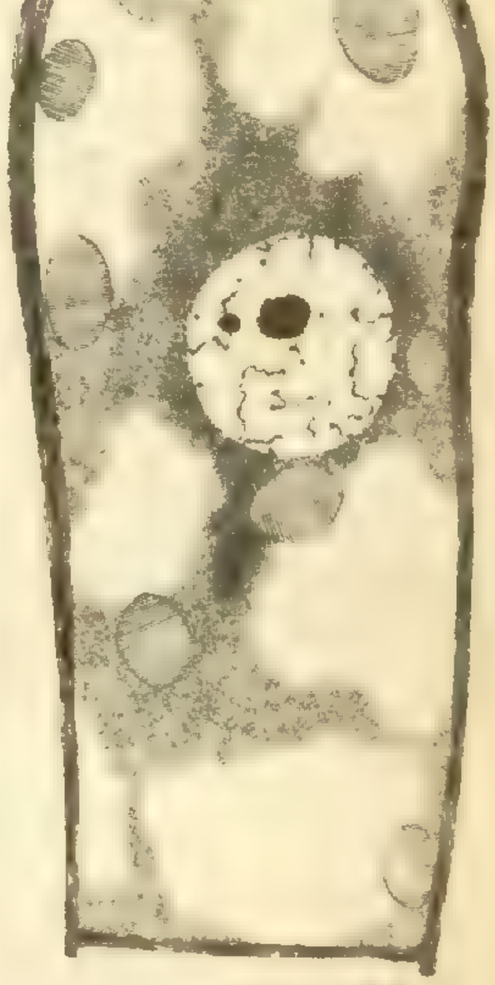

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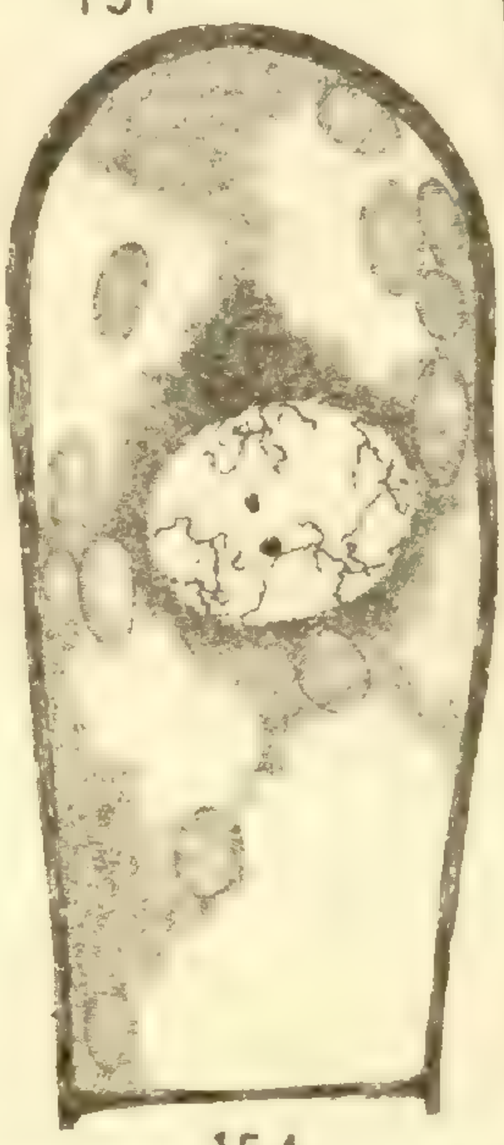

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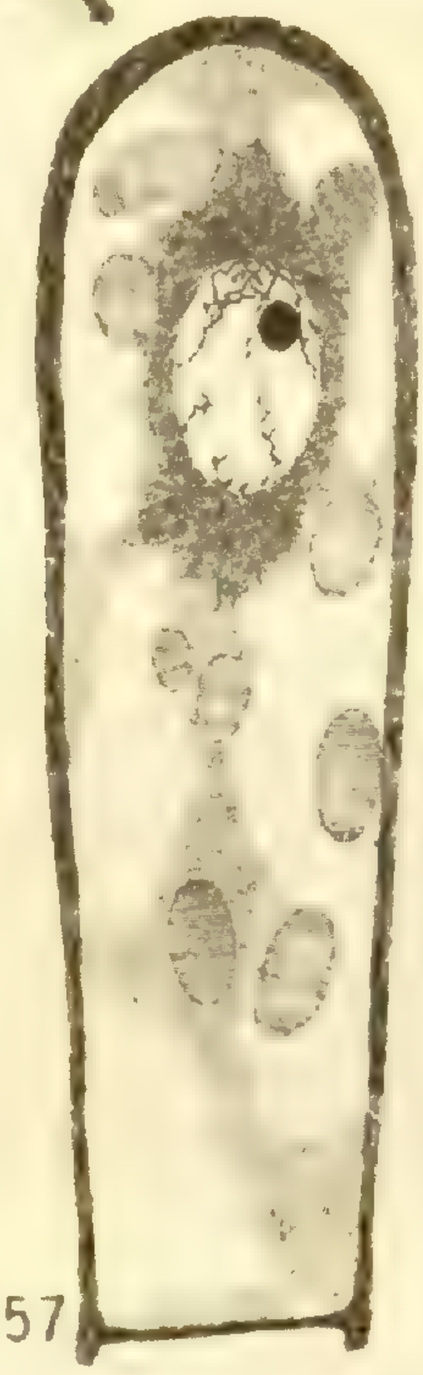

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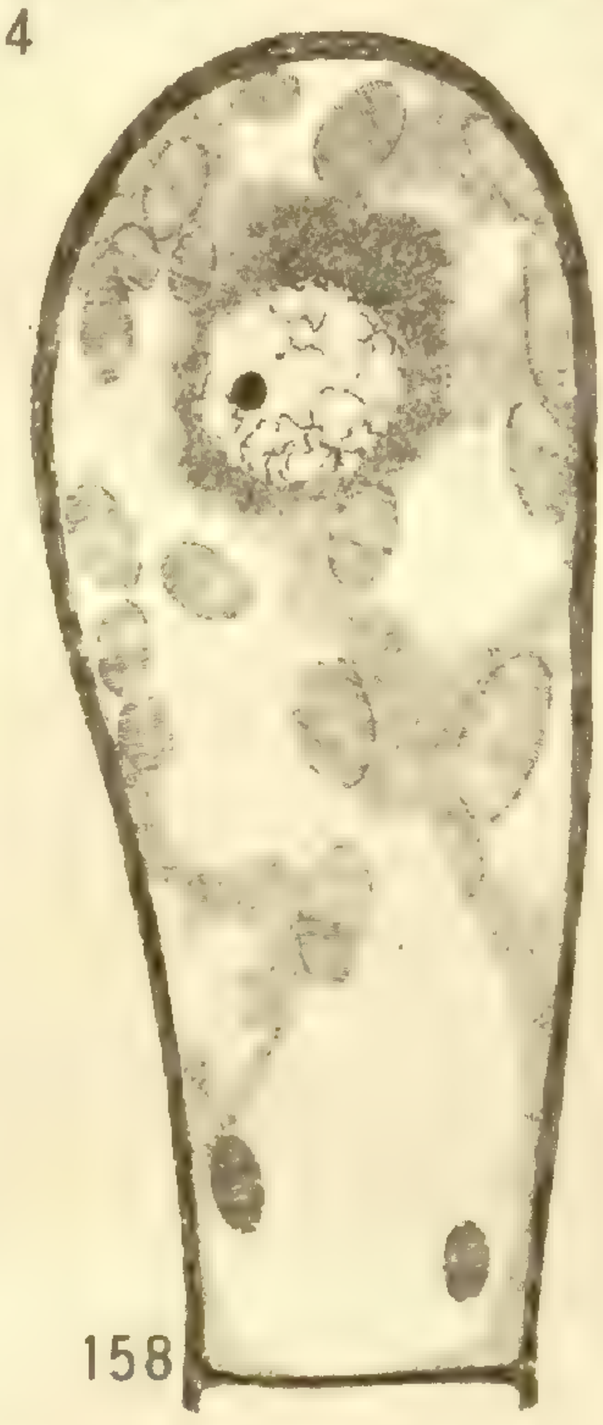

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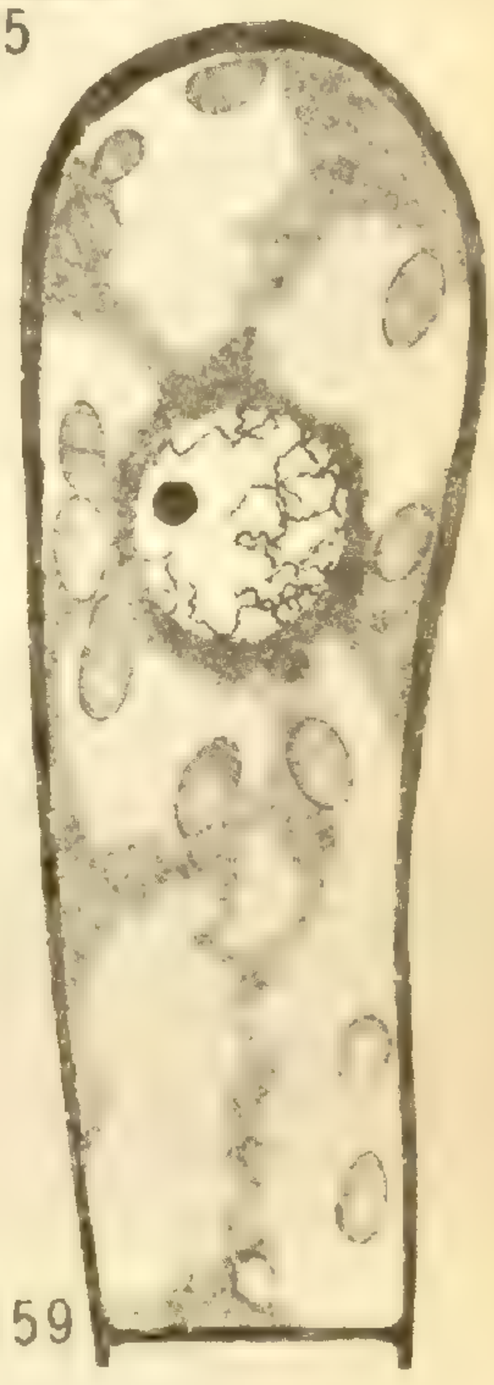

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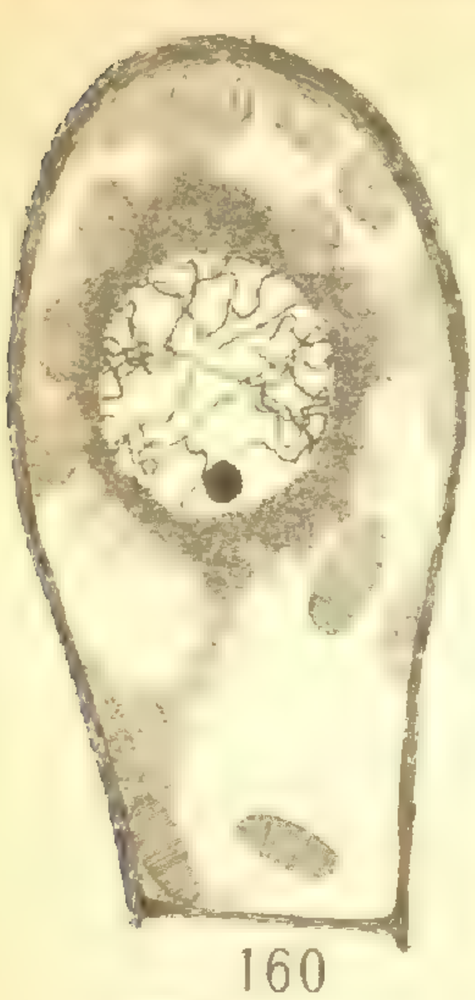

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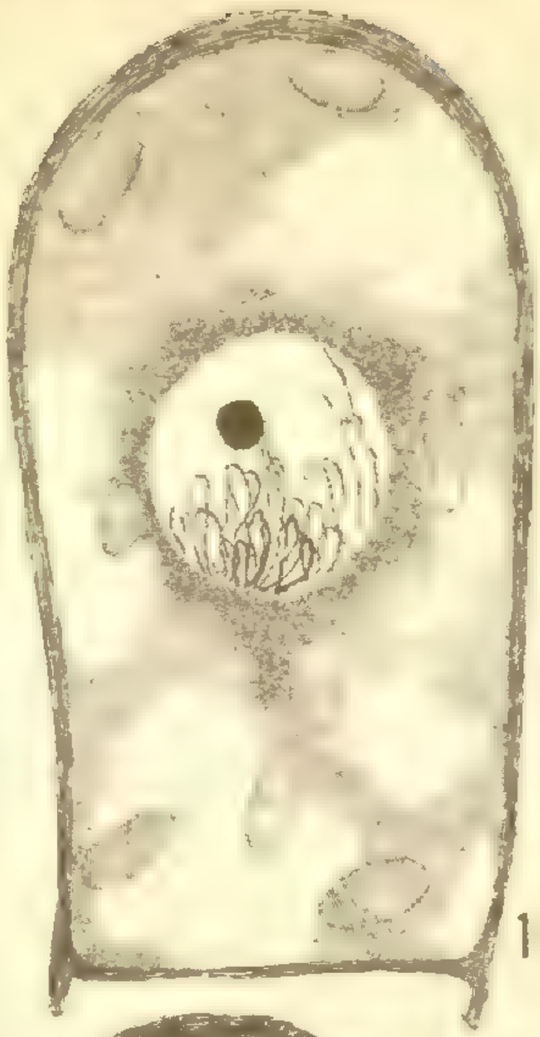

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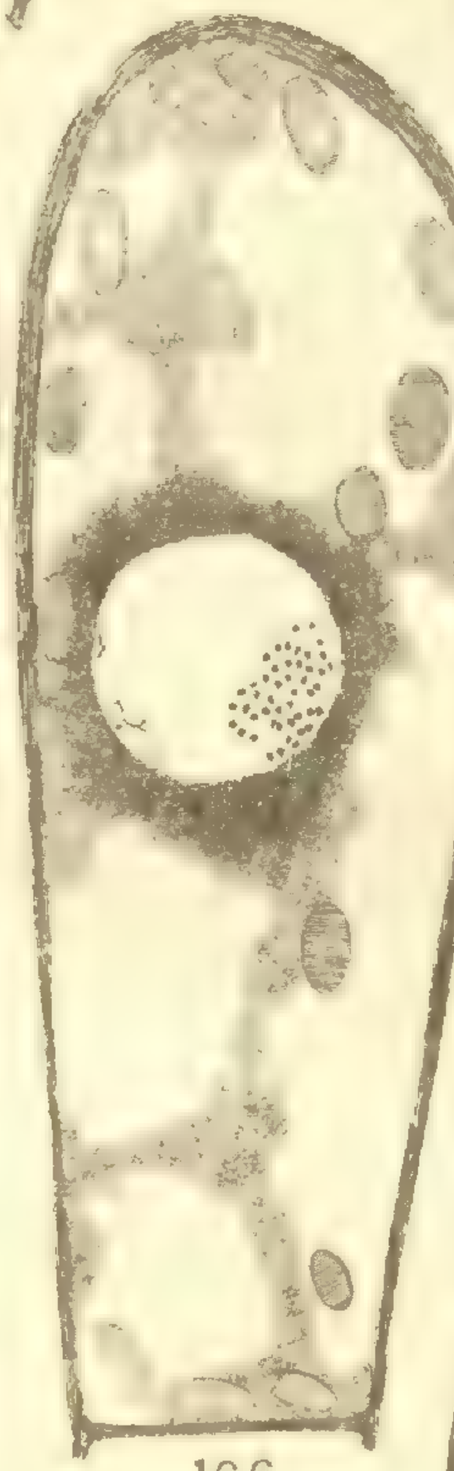

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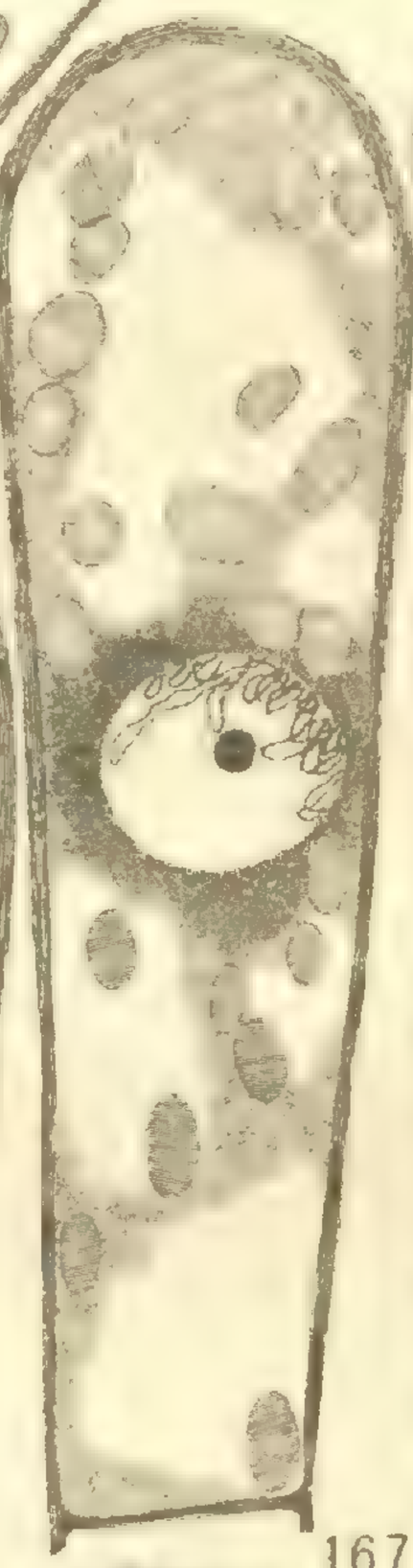

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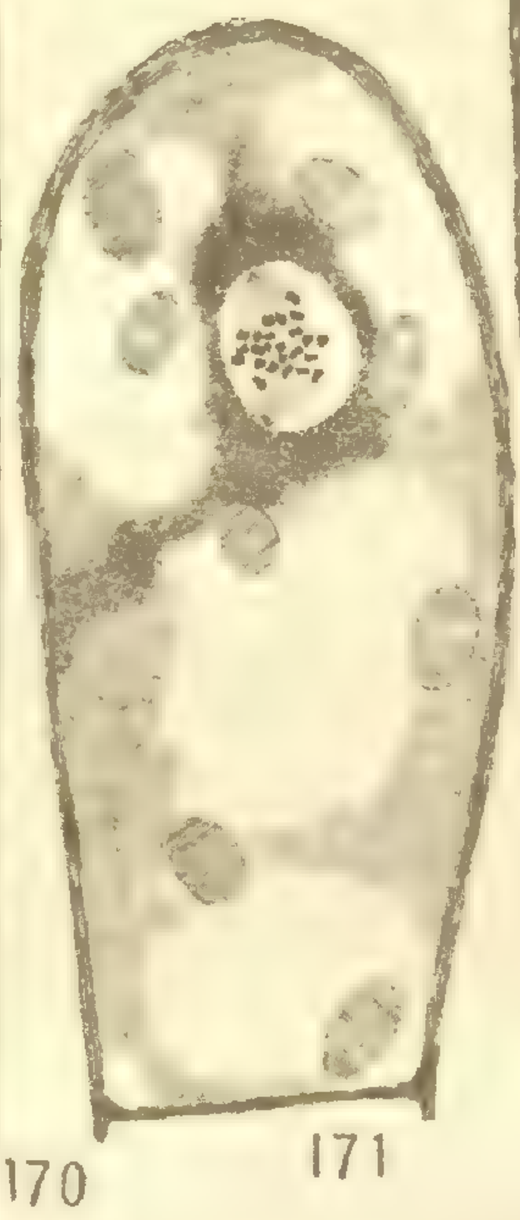

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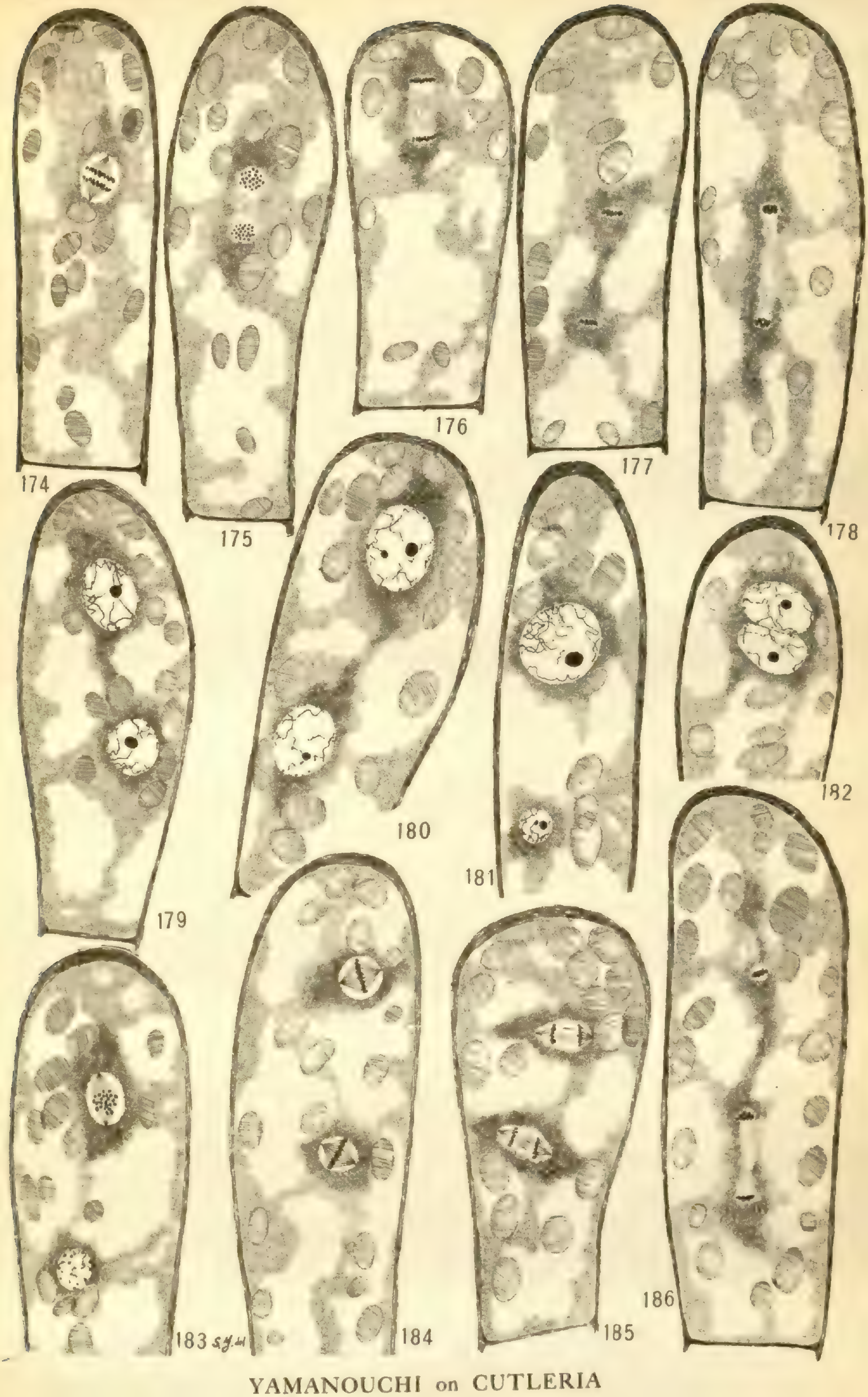

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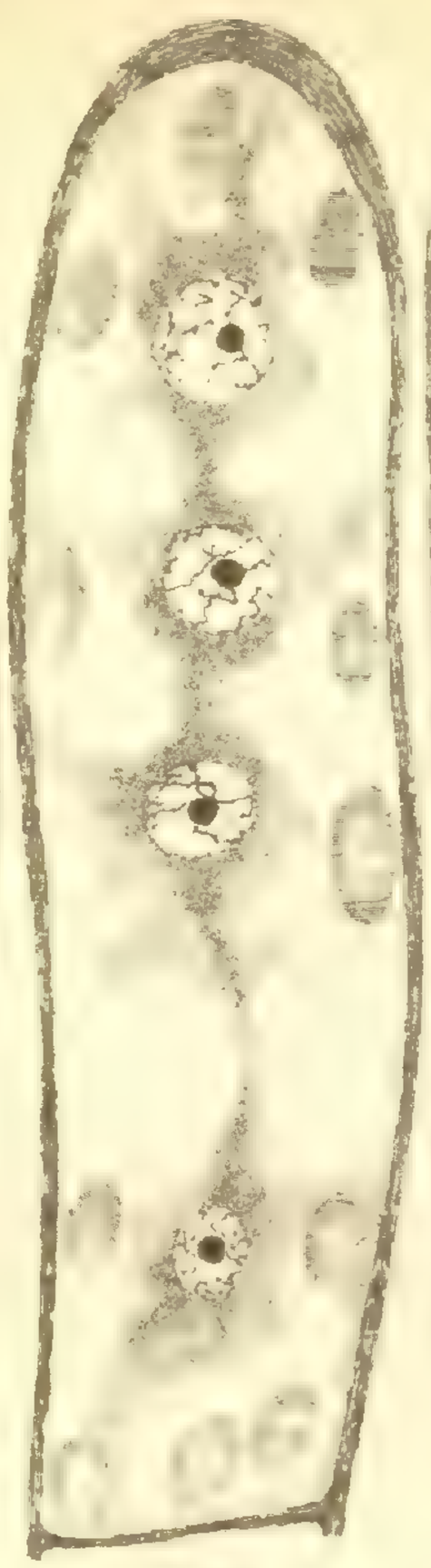

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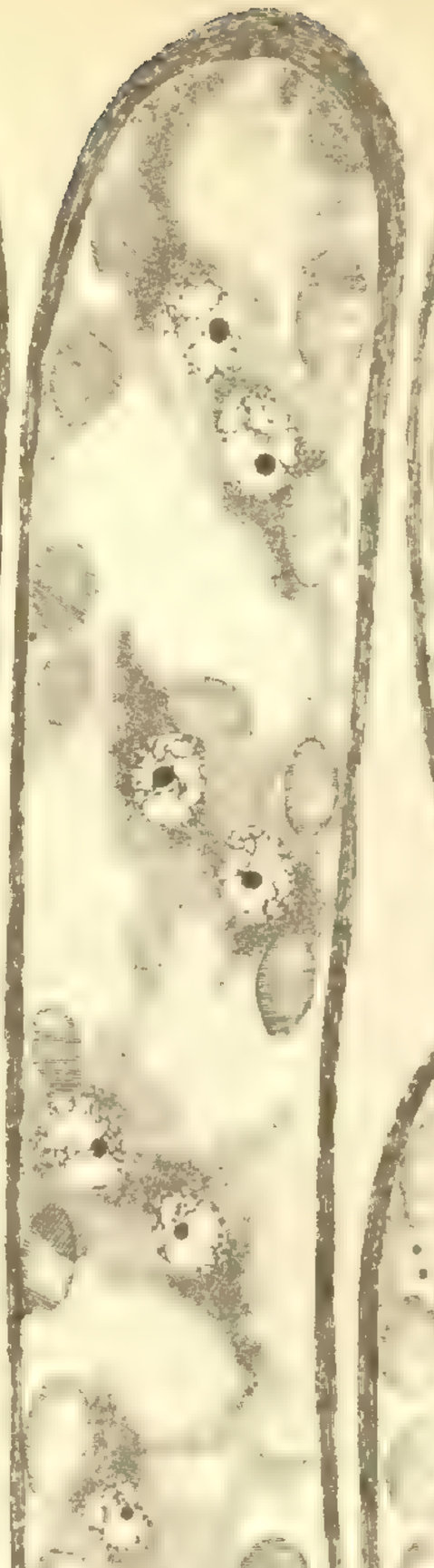

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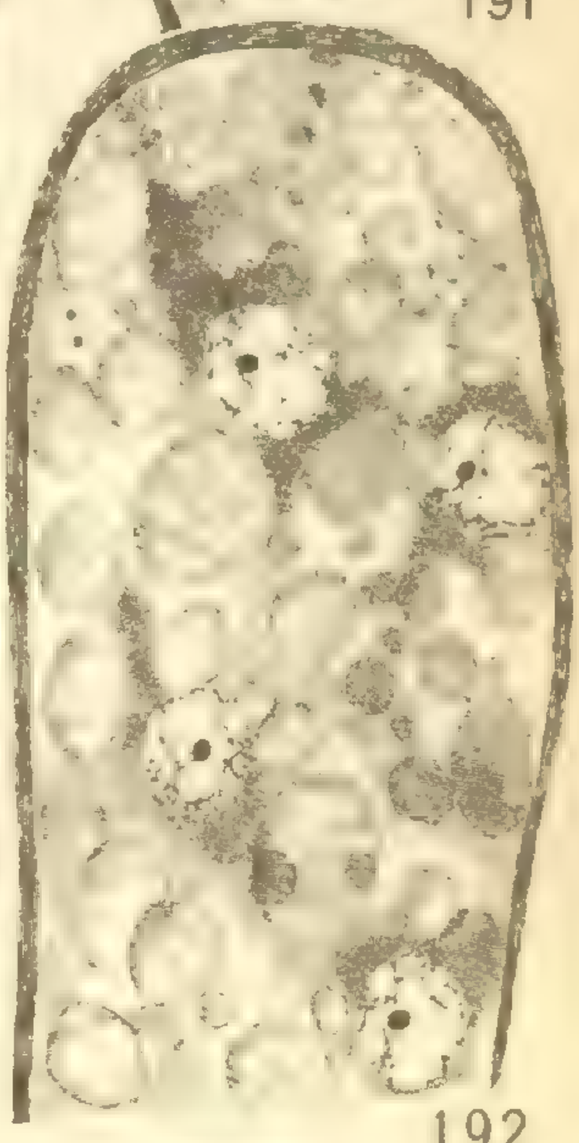

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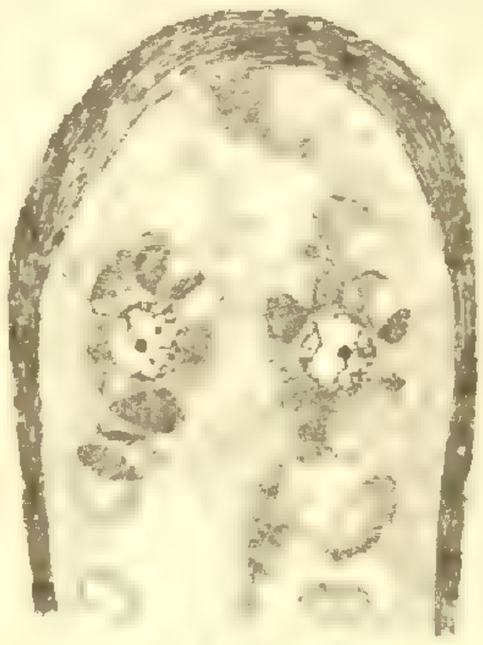

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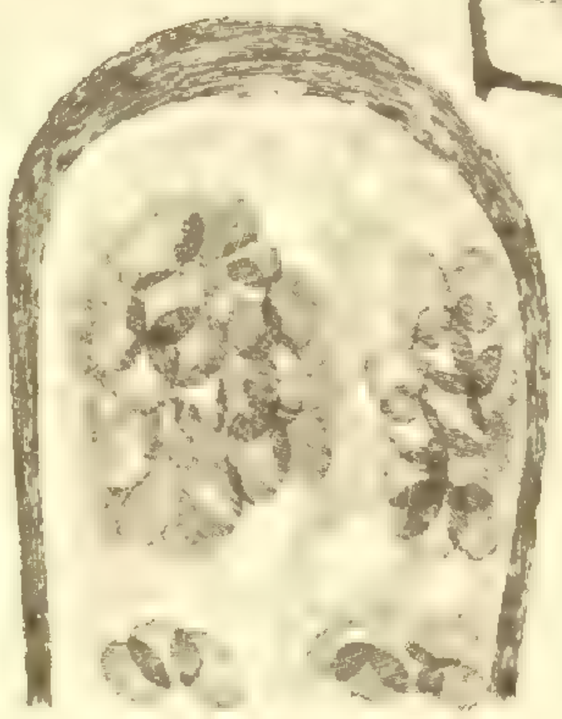

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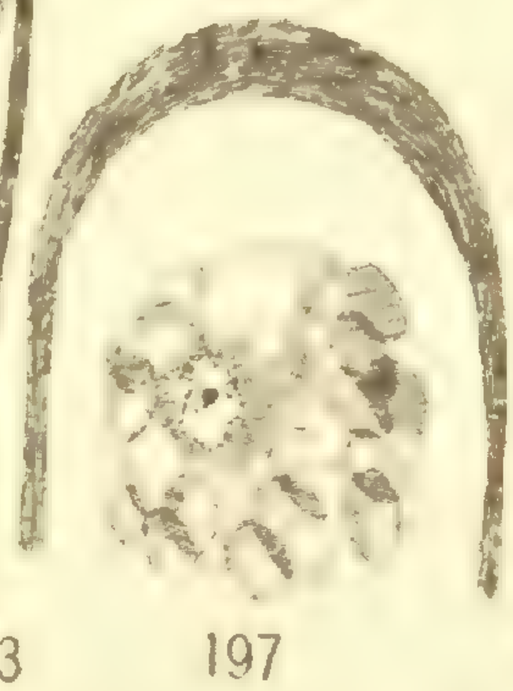

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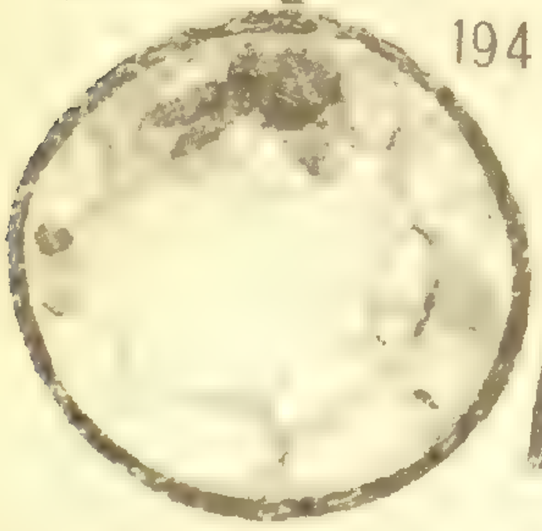

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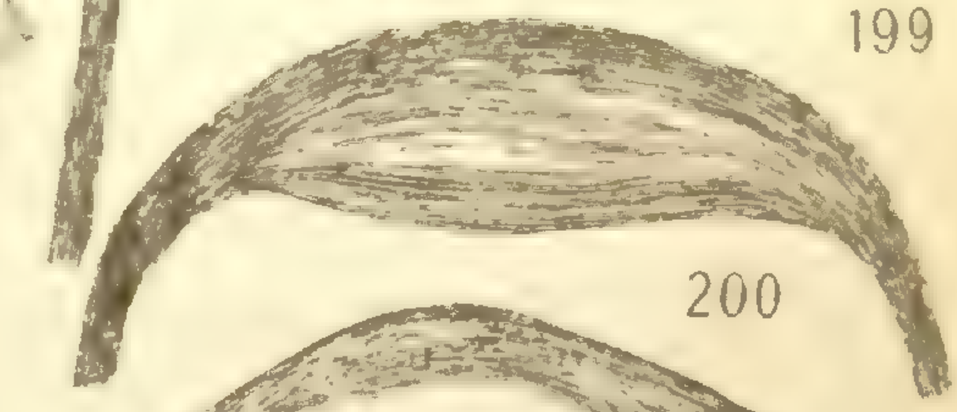

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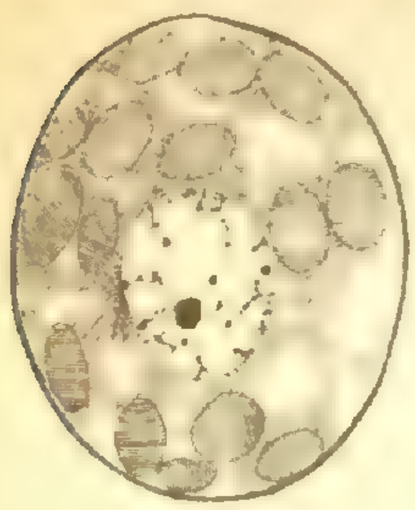
YAMANOUCHI on CUTLERIA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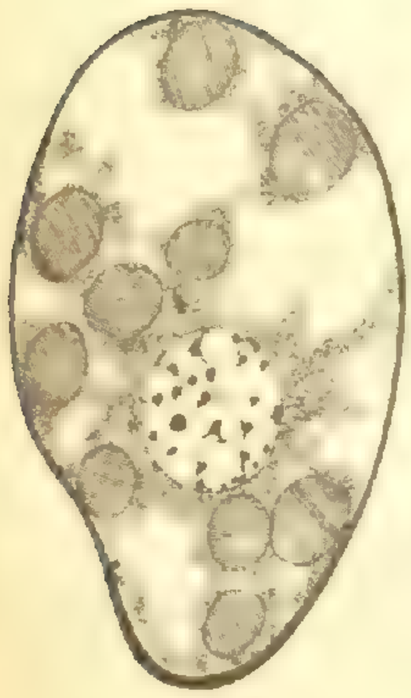
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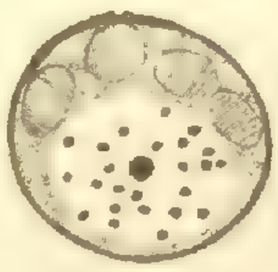
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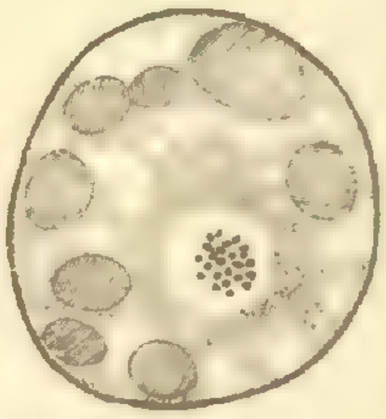
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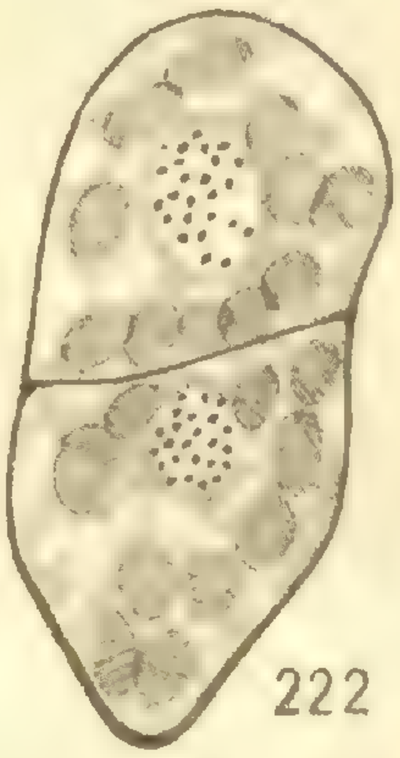
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YAMANOUCHI on CUTLERIA

THE NATURE OF THE ABSORPTION AND TOLERANCE OF PLANTS IN BOGS[1]

ALFRED DACHNOWSKI

The consideration of measured physical habitat conditions,[2] which is desired as a basis for distributional relationships of plant associations, their succession and morphological distinction, and particularly for a theory of physiologically arid habitats, has not rendered clearer the nature of the absorption of plants in bogs and peat deposits. Interest in the study of the absorption and the varying degree of tolerance and resistance of plants growing in Ohio bogs has been coincident with the determination of the quantitative nature of the habitat factors, but it has been only through an appreciation of the subordinate value of the physical habitat factors that attention could be given to the special diosmotic properties of the plants and of the substances absorbed, together with the changes which the penetrating substances produce upon the plants. The changes which the substances undergo internally or externally to the absorbing cell or organ are relationships of equal importance in the problem of nutritive metabolism, but a discussion of them cannot be attempted as yet.

The evidence as to the rôle of physical and biotic habitat factors, derived from study of bog vegetation in its relations to the substratum, temperature, and evaporation, from consideration of the relation of bog vegetation to the chemical nature of peat soils,[3] need not be reviewed here in detail. 'It pointed to something else than merely the atmospheric influences as ecological conditions for the development of bogs and for the selection and growth of plants tenanting such areas.

[1] Contribution from the Botanical Laboratory, Ohio State University. No. 71. Read before the Botanical Society of America at the Washington meeting, 1911.

[2] DACHNOWSKI, A., The vegetation of Cranberry Island (Ohio) and its relations to substratum, temperature, and evaporation. BOT. GAZ. **52**: 1–33, 126–150. 1911.

[3] ———, The relation of Ohio bog vegetation to the chemical nature of peat soils' Bull. Torr. Bot. Club **39**: 53–62. 1912.

The evaporation in a bog forest averages 8.1 cc. daily and shows a close correspondence to the record obtained by others for a beech-maple forest.[4] In a bog meadow the rate (10.9 cc. daily) is less than that for the open campus of the State University (15.8 cc. daily). As far as local atmospheric conditions are concerned, the rate of evaporation is not a sufficient cause to determine succession of vegetation, nor are the differences in the rates efficient limiting factors.

The rôle of substratum temperature is obviously not the most direct factor in southern localities contributing to the causal relation between water requirements of bog plants and available supply. Neither has the coefficient of the differences between soil and air temperatures a greater value in the selection of plants for bog areas, or in their root functions.

The concentration of mineral salts in bog water from various plant associations ranges between 40 and 160 parts per million; the acidity of the solutions varies from less than 0.00075 to 0.004 normal acid, when titrated with NaOH. There seem to be no free "humus" acids. The acid reaction noted can be attributed to adsorption phenomena,[5] especially to the selective absorbent power of the cell colloids of disintegrating plant tissue which retain, as BAUMANN and GULLY[6] have shown, chiefly the basic ions of dissolved salts. The osmotic pressure of the solutions in the various associations is very nearly alike in the several plant zones and about the same as that of lake and river water. The differences cannot be associated with factors limiting the distributional relationships and the activity of plants in bogs.

Variations in the position of the water table do not influence the character of the vegetation, nor do they offer an explanation of the xerophytic structure of the plants, for the peat mat upon which the more typical bog xerophytes and heath associations succeed one another is more often a floating mat and moves with any change

[4] TRANSEAU, E. N., The relation of plant societies to evaporation. BOT. GAZ. **45**: 217–231. 1908.

FULLER, G. S., Evaporation and plant succession. BOT. GAZ. **52**: 193–208. 1911.

[5] CAMERON, F. K., The soil solution. 1911. p. 55.

[6] BAUMANN, A., und GULLY, E., Über die freien Humussäuren des Hochmoores. Mitt. K. Bayr. Moorkulturanst. 1910. pp. 31–56.

in the water table of the lake. In such a mat differences in the rate of the movement of water through peat soil do not exist, and hence are out of the question in the problem of the supply and the rate of removal of water by plants.

The chemical analyses of Ohio peat soils, the data of which appear elsewhere,[7] show wide variations, but there is a certain uniformity in the range. When a correlation between the chemical character of peat and the respective bog vegetation unit is attempted the well defined relations are these:

In poorly decomposed bog meadow peat the percentage of volatile matter is high, the percentage of fixed carbon, nitrogen, and ash is low; the reverse is true for the well decayed peat supporting a bog forest and deciduous trees.

Peat soils from various plant associations in bogs contain the essential mineral salts such as potash, phosphoric acid, and others, in inconsiderable quantities—only a fraction of 1 per cent. The salts, it seems, play only a minor rôle for protoplasmic activities, and in the growth and ripening of bog plants. Tolerance and resistance of plants to bog habitat is not an osmotic relation; it cannot be related to a greater resistance to water absorption produced by high external osmotic pressure, nor, it seems, to the lack of some one salt in the mineral content of the soil or in the plants. The ash content of the wood of bog trees is less than 0.5 per cent, with an occasional maximum of about 1.5 per cent.

The solubility of the coarsely fibrous peat from bog meadows is less than that of peat in more advanced stages of decomposition supporting genetically higher associations of plants. The quantity of nitrites, nitrates, and ammonia is very small and yet amply sufficient to support luxuriant growth. Practically all the substances in solution are transition products of proteins and carbohydrates arising through the action of obligate microorganisms. Bacteriological investigations have shown clearly the importance of biological processes. As a source of food to the microorganisms and in the nature of the organic compounds produced during the partial digestion of the upper layer of the vegetable débris, the substratum constitutes an efficient limiting and selective factor.

[7] DACHNOWSKI, A., The peat deposits of Ohio. Geol. Surv. Ohio, Bull. 16, 1912 (in press).

Now that it has been possible to show the inadequacy of various of the physical environmental relations of plants in bogs to account for the failure of some of the agricultural plants to thrive and for the survival of others; and since differences in light-intensity, in special absorptive powers of roots for peaty substrata, in fungal mycorhiza, and in morphological limitations in the absorption and in the conduction of water do not enter into the problem with the agricultural plants used for the test experiments, it seems timely to consider in more detail the specific rôle of the organic decomposition products in the relation between the required quantity of available water and the quantity absorbed by the plants.

That some sort of regulatory, reciprocal mechanism, acting within certain limits, is of the utmost importance in these species seems evident from the fact that while the presence of structural modifications is generally regarded as reaction in favor of a bog vegetation, the most noteworthy characteristic which enables invading plants to resist the unfavorable conditions is a greater elasticity of functions and perhaps some specific place function. What is the mechanism connected with the failure of many agricultural plants to thrive in peat soils and in solutions of bog water? What critical features, either as products of habitat or congenital variation, do the surviving plants possess to regulate or control the absorption of injurious organic bodies, and what are the pathological aspects which involve dwarfing, leaf-fall, and general senescence in most invading species alien to the habitat?

A knowledge of the limits of functional variation within a known species and its several varieties should prove very essential as to the rôle and the range of the individual and genetic differences in the plants themselves, and the ability of the plants to inhibit the absorption of deleterious bodies, or to neutralize the injurious action of the substratum.

In the present preliminary paper data are submitted which were obtained from experiments in the laboratory with several standard varieties of grain sorghums, alfalfa, and bean. The seeds were obtained from the United States Department of Agriculture through the office of seed distribution. The seeds were germinated in sterilized quartz sand and employed in a manner

described in earlier papers. The physiological tests were made in bog water from the central (cranberry-sphagnum) station on Cranberry Island at Buckeye Lake, Ohio. All experiments were made in duplicate series. Paper-covered "Mason" jars were used containing 500 cc. of untreated bog water. The following selected series in tables I to III is especially suggestive and typical.

The tables show at a glance which of the varieties is the more efficient in counteracting the effects of injurious organic compounds. Not only the relative transpiration quantities but also the morphological effects as shown by the general appearance of roots and leaves bear out the observation that the rate of entrance of water is as high and higher than the transpiration rate. The evaporating power of the air during several of the experiments was relatively high.

Especially in bog water of greater toxicity than that of the date in the above series, the plants were in strong contrast to each other. The rate of growth varied considerably according to the amount of transpiration and to the supply of available water. The decreased permeability of the plasmatic membrane of the root-hair cells favored their efficiency in selective absorption and in growth. When the rate of transpiration decreased, the root tips and the tops made but slight growth. The roots were discolored for some distance from the tip, appeared gelatinous, and not only their surface but the meristematic tissue seemed injured, inhibiting the formation of new laterals. The leaves were short and unfolded imperfectly. At the beginning of the experiment the roots of the stronger plants were able to counterbalance the injurious action to a slight extent; light brown insoluble bodies appeared deposited upon the surface of the roots. In dilute solutions of bog water the roots remained white. Invariably, however, the toxicity was lessened most in plants whose ability to counteract the harmful effects was most pronounced. The plants functioned less readily, and their rate of reaction diminished as the active mass of bacterial products increased.

A characteristic behavior became evident in the increase of green weight of the plants in the dilute solutions, and in the observation that this effect was far from being uniform in all the cultures. The

deleterious action of bog water was, on the whole, less marked upon the tops than upon the roots. Nevertheless the green weight of some of the plants with a lower transpiration value was greater than that of the plants transpiring more strongly. Examples are numbers 3, 5, and 7 in table I; 2 and 5 in table II; 4 and 6 in table III; 7 and 10 in table IV.

TABLE I

TRANSPIRATION DATA OF VARIETIES OF GRAIN SORGHUMS[8] IN BOG WATER
MARCH 6–24, 1910

Variety of sorghum	Transpiration in grams	Green weight produced	Water required for 1 gram of green matter
1. Milo	106.15	2.59	40.95
2. White Durra	91.05	2.18	42.98
3. Dwarf Milo	86.70	2.87	30.17
4. Dagdi Durra	78.95	1.89	41.70
5. White Kowliang	78.32	2.92	26.08
6. Blackhull Kaffir	69.95	1.40	49.85
7. Brown Kowliang	55.65	1.46	37.98
8. Red Kaffir	52.90	1.28	41.34

Atmometer: 25 cc. daily average

TABLE II

TRANSPIRATION DATA OF VARIETIES OF ALFALFA IN BOG WATER
MAY 6–26, 1910

Variety of alfalfa	Transpiration in grams	Green weight produced	Water required for 1 gram of green matter
1. Medicago falcata	11.50	1.48	7.77
2. Var. 16399 (Washington)	11.86	2.28	5.20
3. Var. 23625	8.72	0.99	8.80
4. Var. 9359 (Turkestan)	7.32	0.59	12.40
5. Sand Lucerne 20457	11.93	2.21	5.40

Atmometer: 18.9 cc. daily average

It is quite generally known that rapid growth is usually accompanied by active respiration, and hence slowly developing plants are able to increase in dry weight upon a smaller quantity of water absorbed and transpired. It seems clear from the normal appearance of the roots of these plants, that the injurious substances have an entirely different effect upon some varieties of the plants with

[8] BALL, C. R., The history and distribution of sorghum. U.S. Dept. of Agriculture, Bur. Plant Industry, Bull. 175, 1910.

the smaller transpiration value from that observed in others. The marked difference is undoubtedly due to the nutritive value of the assimilable organic compounds. This particular feature of variability in nutritive metabolism is so characteristic and strik-

TABLE III

TRANSPIRATION DATA OF SPECIES AND VARIETIES OF BEANS IN BOG WATER
FEBRUARY 24–MARCH 11, 1910

Species and varieties	Transpiration in grams	Green weight produced	Water required for 1 gram of green matter
1. Dolichos 22025.....	150.68	3.75	40.18
2. Dolichos 8542.....	99.54	1.52	65.61
3. Phaseolus mungo var. 18310.	66.46	1.34	49.59
4. Var. 17096.....	69.98	2.32	30.16
5. Phaseolus mungo.....	56.35	1.24	45.32
6. Guar.....	36.57	1.21	32.23

Atmometer: 7.3 cc. daily average

TABLE IV

TRANSPIRATION DATA OF WHEAT PLANTS IN SOLUTIONS OF STERILIZED BOG WATER AND PEAT, INOCULATED WITH BOG BACTERIA
MARCH 31–APRIL 15, 1910

Culture	Transpiration in grams	Green weight produced	Water required for 1 gram of green matter
1. C. 19 b.+f.....	12	1.16	10.37
2. C. 15.....	8.90	0.80	11.12
3. D. 20.....	14.90	1.14	13.07
4. C. 13.....	13.08	0.94	13.91
5. C. 7.....	15.65	0.98	15.96
6. C. 16.....	15.25	0.93	16.39
7. C. 19 (fungus).....	17.93	1.60	11.20
8. C. 17 (fungus).....	17.40	1.01	17.22
9. C. 9.....	18.07	1.06	17.04
10. C. 21 (fungus).....	27.33	2.36	11.58
11. Alder tubercles.....	50.31	2.20	22.86
12. Mixed culture of above....	67.48	1.92	35.14

Atmometer: 11.7 cc. daily average

ing in agreement with the several experiments which were conducted, that analyses with reference especially to the ratio between the carbon and nitrogen content of the plants are much to be desired. Experiments on the availability of nitrogen in peat have been made by a number of workers, but mostly upon sun-dry or

kiln-dry peat, the solubility of which in water is very low. The results confirm, however, both an increase in the production of dry matter in plants, and of dry matter relatively richer in the amount of nitrogen, as compared with the percentage in plants from soils lacking peat.[9]

Additional evidence of a similar nature is derived from experiments of more recent date with pure cultures of isolated bog organisms growing in sterilized solutions of bog water and peat (table IV, nos. 7 and 10), and from the preliminary work upon peat composted with the bacterial life from stable manure. They confirm the earlier experiments and also demonstrate the ability of some mycelial bog fungi and the organisms in alder tubercles[10] to increase transpiration and green weight of wheat plants about 200 per cent above that in untreated bog water. Normal appearance is here associated with a uniformly higher absorption of the solution, amount of transpiration, and green weight produced, and with the healthy condition of roots and leaves. The wheat plants in the cultures have the usual osmotic pressure isotonic with about a 0.2 to 0.3 normal potassium nitrate solution. Difficulty in absorption and tolerance or the xerophytism in bog plants do not seem to be correlated with high osmotic pressure.[11]

The point of most importance which should be noted in this connection is the obvious difference in the water requirements of the plants. Water and its solutes, whether organic compounds or inorganic salts, are as a general rule taken up in a different ratio from that existing in the substratum. The existing differences in the various colloids of cells would naturally tend toward inequalities in the amount of water or solutes absorbed and held by the tissues of the different varieties of species; the diosmotic properties of the protoplasmic membrane, differing according to the species

[9] HASKINS, H. D., The utilization of peat in agriculture. Massachusetts Sta. Rept., pt. 2:39–45. 1909.

LIPMAN, J. G., Report of the soil chemist and bacteriologist of the New Jersey Agricultural Experiment Station. 1910. pp. 188–195.

[10] SPRATT, E. R., The morphology of the root tubercles of *Alnus* and *Elaeagnus* and the polymorphism of the organism causing their formation. Ann. Botany **26**: 119–128. 1912.

[11] FITTING, H., Die Wasserversorgung und die osmotischen Drukverhältnisse der Wüstenpflanzen. Zeitschr. f. Bot. **3**:209–275. 1911.

used as an indicator, would further determine the difference and variability in absorption, resistance, or tolerance. Inasmuch as the amount of mineral salts in bog soils and the amount used in the growth of bog plants is very small, and since the lack of larger quantities is not a factor in the succession of bog associations, the most fundamental distinction is that which controls the supply of available water. A method of determining the ratio between ash and the yield in organic compounds on the basis of the water requirement of plants for the period of their growth would have the merit of convenience, and, it must be admitted, the accuracy which is often questionable in the unit employed and as preferably expressed in agricultural literature. The unit of water requirement now used in agricultural texts for ten different economic species is 450 pounds of water for one pound of dry matter produced. Data of that character do not place the classification and comparison of soils, correlations with fertility or with age of plant, maximum growing period, and seasons on a measurable basis. The unit is numerically inaccurate and does not express the fundamental and causal relations.

Experiments upon the transpiration value of bog plants in relation to structure and habitat, to be published later, have shown that the data cannot always be expressed satisfactorily in the gm^2h system. Transpiration is a reciprocal relation. It is affected by the conditions which react upon the absorbing roots, and it is associated with chlorophyll activity and the absorption of carbon dioxide in the vertical gradient. Transpiration in the lower, more humid stratum of a bog meadow is often slight for days at a time. The luxuriousness of the vegetation and the amount of dry matter produced do not vary in this case with the transpiration quantity, but with protoplasmic permeability and the specific metabolism, permitting of exchanges by solubility, and with the active enzymic agents within the cells which effect the assimilation or the destruction of the substances in the external medium. Whatever the cause of the differential permeability,[12] solubility

[12] CZAPEK, F., Über eine Methode zur direkten Bestimmung der Oberflächenspannung der Plasmahaut von Pflanzenzellen. Jena. 1911.

LEPESCHKIN, W. W., Zur Kenntnis der chemischen Zusammensetzung der Plasmamembran. Ber. Deutsch. Bot. Gesells. **29**: 247–260. 1911.

of the substances in the medium and in the plasmatic membrane is prerequisite to penetration (osmosis) into the living cells.

In previous publications on the factors by which the present bog vegetation is determined the writer pointed out that different species of cultivated plants show marked differences in the degree of sensitiveness to the toxic conditions of a bog habitat. That the stunted plants in these experiments have not lost their capacity for absorption and growth can be readily demonstrated. The plants resume their natural functions as soon as they are placed in dilutions less fatal in its effects. In contrasting the differences in physiological activity it was further shown that various phases of absorption and transpiration resulted from the progressive addition to the medium of chemically inert filtering materials. Types of soil were used ranging from the weathering products of soil-forming rocks to the completely oxidized products characteristic as the final residue. Incidentally it was shown that the normal growth of the plants in the uncontaminated soils was replaced by an abnormal retardation. In the main the study indicated that upon extraction of the injurious substances by means of insoluble adsorbing bodies, not only the differences between different species as to their tolerance and resistance were less pronounced, but also the differences in toxicity existing between the several zones within the same habitat. The selective action of the habitat was shown to be greatly diminished upon the removal of the injurious organic substances accumulating in the peat substratum. The conclusion was drawn that the relative power in bog plants for absorbing or rejecting the injurious constituents of bog soils and bog water was therefore the limiting factor, controlling the survival value of invading species and of plants native to the habitat. The roots of bog xerophytes are not much shorter than those of other plants; the lateral roots develop extensively, and the prevalent direction of root growth is horizontal rather than downward. This reaction cannot be regarded as one due to low soil temperature or to a slight oxygen content. The inhibitory factor for root growth which increases with depth is the reducing action of the substratum and the incomplete disintegration of organic compounds. It is now well known that certain root enzymes are oxidizing agents

which assist in the destruction of deleterious compounds in soils of an organic nature, and that the oxidizing action becomes lessened when the injurious organic substances are in excess. The wide variations in this functional reaction are probably of greater importance than external factors. It seems a tenable hypothesis, therefore, that the survival or the extinction of invaders may depend more upon the degree of functional plasticity than is generally admitted.

The experiments here cited furnish nothing more than an indication of the relative importance of some of the factors involved. The weight of evidence is obviously incomplete, for numerous important considerations have received no attention whatever in the present paper. The problem of absorption is not one of simple solution, but an intricate and coordinated process, and much needs to be known of the energy relations between plants and habitat and the organization of the protoplasmic membrane of absorbing organs. From the present study the following relations may be summarized:

1. Physiological investigations of peat soils have brought out clearly the fact that the character of the obligate bacterial flora and the nature of the organic compounds produced form a very important factor in the relative fertility of peat soils, in the causes of vegetation succession, in the distributional and genetic relationships of associations, and in the characteristic xeromorphy of both ancient and modern bog vegetation.

2. In view of the widely differing behavior of agricultural varieties in a bog water solution, and the interesting observation that the plants respond differently to the same solution, the conclusion is inevitable that here the source of the difference must logically be looked for not in the solution alone, but in the condition of the plants as well.

3. Since certain of the organic compounds eventually penetrate the protoplasmic membrane of absorbing organs and inhibit growth, it is evident that much importance must be ascribed to the influence exerted upon the plasmatic membrane, to the consequent differences in its diosmotic properties, and to the pathological changes induced which accompany the absorption of the injurious substances.

4. Some plants in contact with peat soil solutions may cause the organic constituents to be precipitated in an insoluble form.

5. In other plants the different organic carbon and nitrogen compounds arising in peat through the activity of microorganisms may be absorbed and assimilated. The chemical formula and transpiration data alone afford no indication of the physiological importance of the substances, hence the nutritive value of these compounds should be estimated on the basis of the total water requirement of a plant during its period of growth and the ratio between carbon, nitrogen, and ash in the plant.

6. The phenomena of absorption and tolerance of plants in bogs deal plainly not with osmotic pressure relations so much as with considerations of the permeability of the absorbing protoplasmic membrane, its power of endurance, and its ability by enzymic action either to absorb and assimilate or to transform injurious bodies into insoluble, impermeable compounds.

7. The organic disintegration substances in peat soils, while inhibitory to agricultural plants, have little or no effect upon certain xerophytic plants. It is concluded, therefore, that they may be positive forces not only in producing the natural succession of vegetation in bogs, but also in determinating xeromorphy and the associated relation of the members, within each group, which best succeed upon peat deposits. These organic substances play the differentiating rôle and are a cause of the infertility of peat deposits even when the amount of air and water in the soil is abundant and the temperature and humidity conditions are favorable to growth.

It is needless to point out that these facts have an important bearing on the agricultural exploitation of peat deposits and on the subject of the proper value of peat land to agriculture.

It is a pleasant duty to record my thanks to Mr. M. G. DICKEY and Mr. M. COROTIS for their assistance in obtaining the transpiration data in tables I to III.

BOTANICAL LABORATORY
OHIO STATE UNIVERSITY

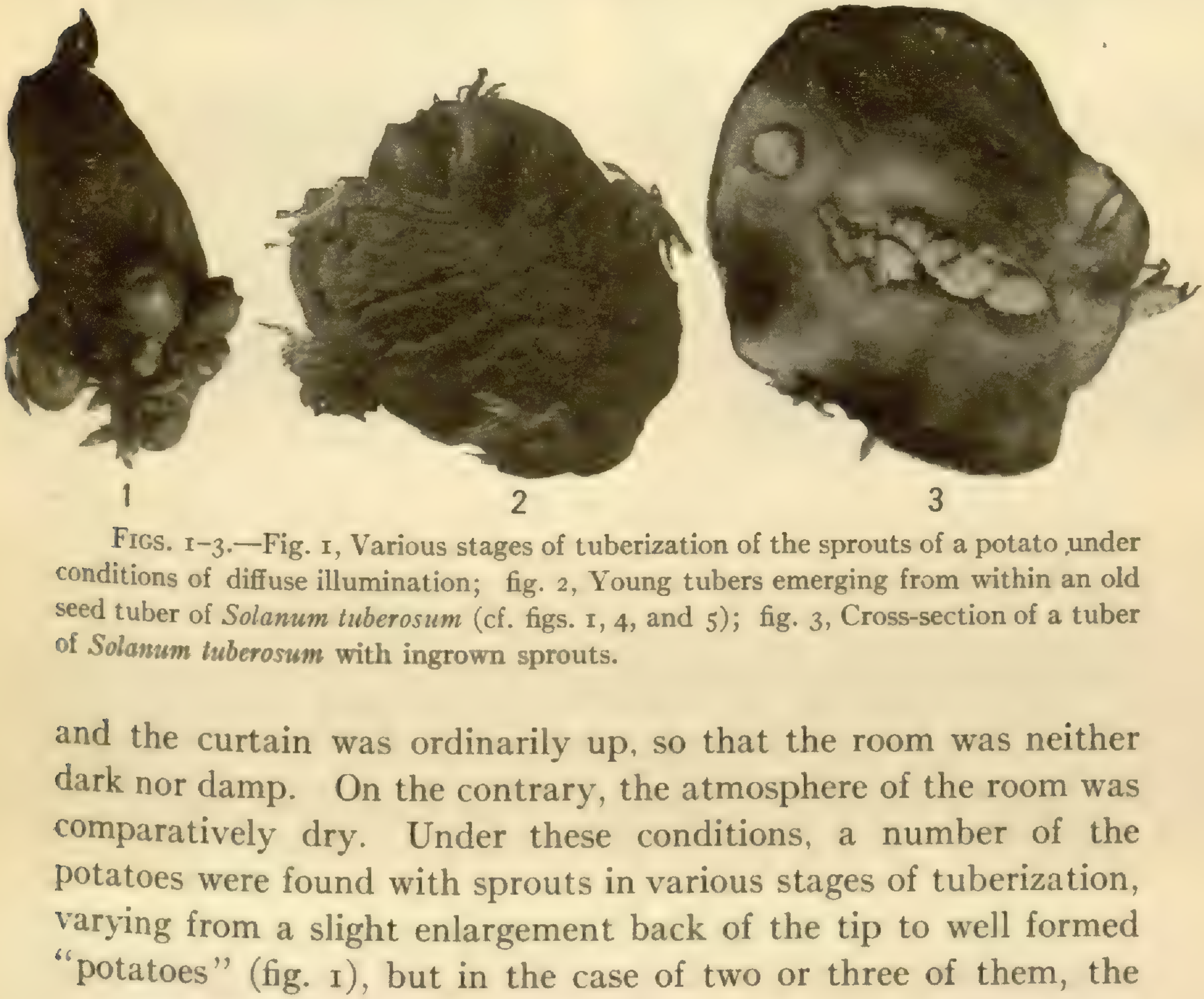
INGROWING SPROUTS OF SOLANUM TUBEROSUM[1]

C. STUART GAGER

(WITH PLATE XXXVI AND SIX FIGURES)

Description

As is well known, it is not at all uncommon to find tuberization of the sprouts on potatoes kept over winter in a cellar. The fact is commonly attributed to the absence of light and the dampness of the cellar. In the late fall of 1907, a large basket of potatoes, of the "Green Mountain" variety, was placed, for want of a cellar, in an unheated chamber. There was one east window in the room,



FIGS. 1–3.—Fig. 1, Various stages of tuberization of the sprouts of a potato under conditions of diffuse illumination; fig. 2, Young tubers emerging from within an old seed tuber of *Solanum tuberosum* (cf. figs. 1, 4, and 5); fig. 3, Cross-section of a tuber of *Solanum tuberosum* with ingrown sprouts.

and the curtain was ordinarily up, so that the room was neither dark nor damp. On the contrary, the atmosphere of the room was comparatively dry. Under these conditions, a number of the potatoes were found with sprouts in various stages of tuberization, varying from a slight enlargement back of the tip to well formed "potatoes" (fig. 1), but in the case of two or three of them, the

[1] Brooklyn Botanic Garden Contributions. No. 5. The substance of this paper was given before the Botanical Society of America on December 29, 1911.

sprout-tubers appeared to be emerging through the skin from within the potato (fig. 2). Closer observation and dissection disclosed the interesting fact that at least a quarter or a third of the potatoes, of which there was about a bushel in all, had ingrowing sprouts. The condition is well illustrated in fig. 3, which is a typical cross-section.

On careful dissection of many of the tubers, the ingrowing sprouts were found to ramify in every direction throughout the

FIG. 4.—Tubers of *Solanum tuberosum* with ingrowing sprouts: the figure at the right shows the ingrown sprouts emerging through the skin; the figure at the left is of a dissection, showing rootlets, the marked development of lenticels, and the tuberization of some of the branches of the ingrown sprouts within the old tuber (cf. figs. 2 and 5).

tissue of the potato. The atrophied and etiolated bud end retained the characteristic nutation curvature, but the sprout was frequently more or less enlarged just back of the tip (figs. 4 and 5). Lenticel-like openings were well developed in the epidermis of the sprouts, often giving them the appearance of a cylindrical file.

Numerous fibrous roots grew out from the branches, and they seemed, for the most part, to be confined in their growth to the channels made by the stem. As is clearly shown in the right hand

potato of fig. 4, the internal sprouts would often grow through the skin and emerge at various points.

The branches tuberized freely, and it was not uncommon to find five or six, or even more, well formed, but pure white, tubers of various sizes entirely within the old tuber. In some cases, as in the right hand specimen of fig. 5, the branches were only imperfectly tuberized, and the tip retained its nutation curvature. Often, as noted above, the young tubers, like the unswollen branches, had pushed through the skin of the potato and, where exposed to the air, had developed a characteristic brown epidermis (fig. 4).

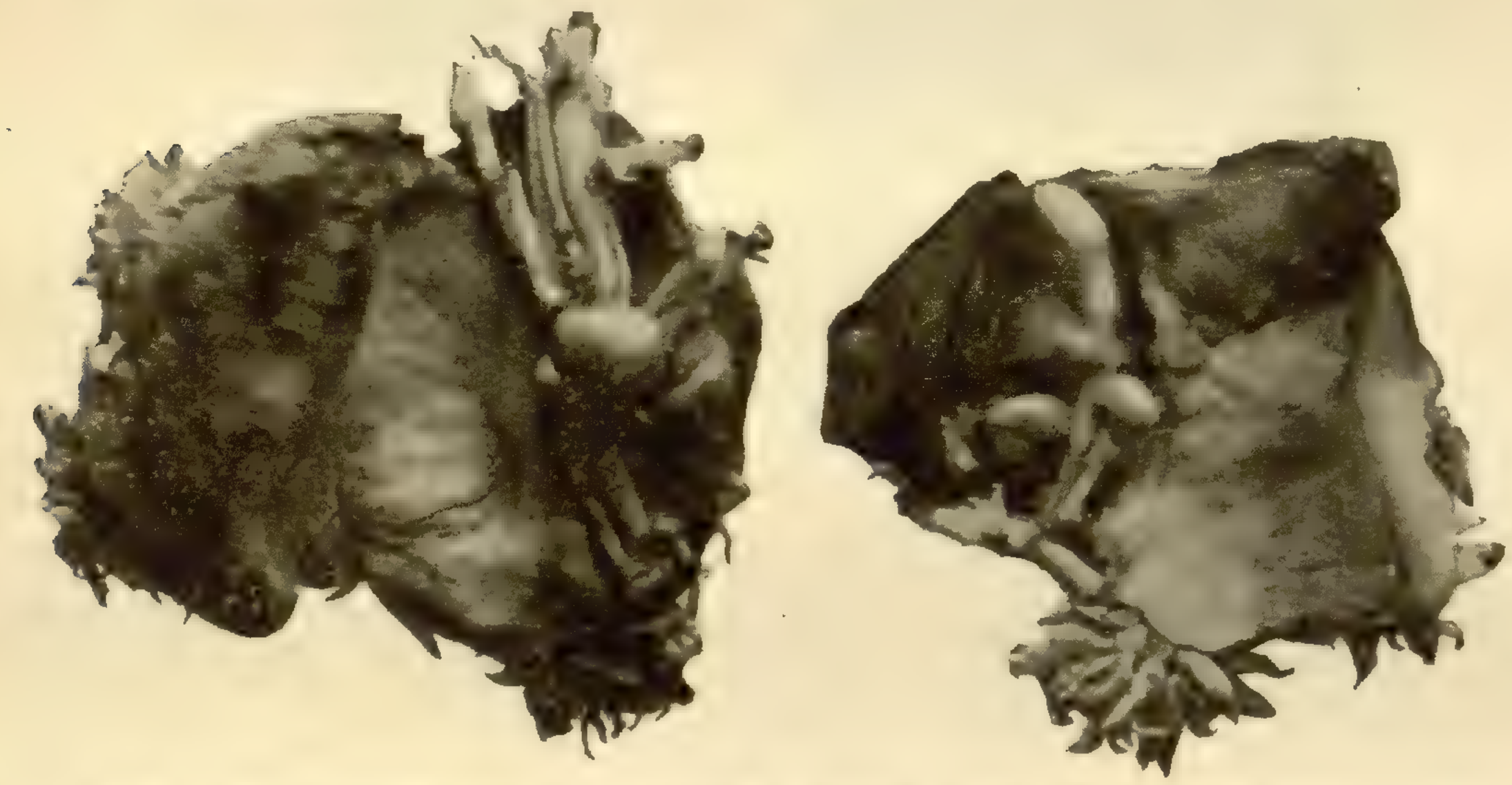


FIG. 5.—Dissected tubers of *Solanum tuberosum*, showing various stages of tuberization of branches of ingrown sprouts, both within and without the seed tuber (cf. figs. 2 and 4).

In many instances there was every *appearance* of a reversal of polarity of the sprout. This is clearly shown in fig. 6, which illustrates two "eyes," the one at the left of a normal potato, the one at the right of one of the abnormal ones. What has occurred in the latter *appears* to be just the reverse of what took place in the former: roots occur at the distal end of the sprout, where we would ordinarily expect the terminal bud, and the numerous branches appear to have developed from the proximal end of the sprout. Whether this is actually the case or not one hesitates to say. It is possible that the entire shoot system, shown at the right in fig. 6, may have developed from a sprout whose tip turned through 180°

toward the surface of the potato and penetrated the parent tuber from without. But it is only the a-priori improbability of a reversal of polarity that makes the writer hesitate to declare it. The evidence clearly indicates it, but the evidence is not all in.

FIG. 6.—Sections through sprouting tubers of *Solanum tuberosum:* at the left, a normal "eye"; at the right, an "eye" with sprouts ingrown and indicating a reversal of polarity of the branch.

Discussion

What caused the ingrowing of these sprouts it is difficult to say. The fact that the potatoes were stored in a room where the air was much drier than that of cellars, where potatoes are usually kept, suggests that the low humidity was at least a contributory cause. But equally interesting is the question of how the sprouts made their way through the tuber. Were the channels through which they grew formed by the digestion of the potato tissue by an enzyme secreted by the tip of the sprout; or did the channels result merely from the mechanical pressure of the sprout as it elongated?

It will be recalled that a similar problem arose in connection with the endogenous emergence of lateral roots. Considerable difference of opinion has existed on this question. The first physiological study of the emergence of lateral roots appears to have been made in 1871, by REINKE (9), who stated that the channel

through the cortex was digested by a substance secreted by the emerging root. The same conclusion was reached later by VON HÖNE (**12**) and by VAN TIEGHEM (**11**). Neither REINKE'S nor VAN TIEGHEM'S figures, however, show evidence of enzymatic action. In 1896 CZAPEK (**1**) reported that he found in the excretions of the roots of higher plants no evidence of any enzymes. If they are present, the amounts are too small to be detected. PFEFFER has declared for a mechanical *modus operandi*, aided by some activity on the part of the cortical tissue.

In 1894 PEIRCE (**6**) found that the roots of *Vicia* and *Pisum* penetrated living tissue by mechanical pressure, unaided by enzymes. He also states that the radicle of *Pisum* could enter through the uninjured periderm of a potato from the outside. In 1903 OLUFSEN (**5**) reported a confirmation of PEIRCE'S results, but POND (**8**) was unable to confirm them, and reported negative results also for *Vicia Faba* and *Lupinus albus*. When the periderm was wounded, the radicles of these seedlings entered easily and penetrated the parenchymatous tissue. When the periderm was unwounded, the radicles deeply indented the surface, but never pierced through. Microscopic examination showed that the periderm cells, and, to a less degree, the hypodermal cells also, were compressed, but there was no evidence of corrosion. "The advancing root formed callus, but when the periderm is wounded the callus does not form. . . . . "

In one of POND'S experiments a potato tuber was cut in two and the outer surfaces placed together and held firmly in this position by string. Then a channel was made in one half to within a few millimeters of the skin, and the radicles of seedlings inserted. The whole was then incased in gypsum. The radicles perforated the periderm of the first half from the inside, and were thus brought into contact with the outside of the periderm of the other half, but this they failed to penetrate. From these observations POND concludes that the mechanical push is too weak to accomplish penetration from without. "Microscopical examination of the flesh of a potato showed no evidence of any digestive action."

In a similar manner POND found that an elongating radicle of *Lupinus albus* was unable to penetrate through the uninjured

epidermis of another *Lupinus* radicle. The second radicle was always deeply indented, but no signs appeared of corrosion of the surface. If the surface was even very slightly wounded, as for example by pricking it with a fine glass point, then the other radicle easily entered and passed entirely through without callus formation. The penetrating root, however, was never found to pass through the central cylinder, but always around it, thus indicating more resistance than that offered by the cortex. The cylinder was indented, but there was no evidence of corrosion of its cells. Starch grains did not appear digested either by autolysis or by the entered root. The results of mechanically forcing a glass rod into the tissue could not be distinguished from those produced by an entering radicle. The conclusion drawn was that the mechanical push was not sufficient to pierce the cuticle from the outside, and that "if the radicle or the lateral root secretes an enzyme, such enzyme has no digestive action upon the cuticle."

As in the case of the roots, so with the potato, the course of procedure for a solution of the problem is clearly indicated. If the channels were the result of enzymatic action we would expect to find, first, in the tips of the sprouts an enzyme able to digest the potato tissue; second, evidence of enzymatic action in the tissue itself; third, absence of any evidence of mechanical pressure; and finally, we might expect to find the epidermis of the ingrowing sprout modified in the direction of glandular epithelium. If the sprout merely pushed its way through the tissue of the tuber, we would find no signs of enzymes or of enzymatic action, but rather positive indication of mechanical pressure.

Physiological and anatomical study

A considerable quantity of tips of the ingrowing sprouts was given to Professor WILLIAM J. GIES, of Columbia University, who kindly offered to have them tested for enzymes. While waiting for a report on this test, microscopic sections of the sprouts were examined, to see if there was any modification of the epidermis in the direction of a glandular epithelium, such for example as that on the scutellum of the embryo of *Zea Mays*. As is clearly shown in *A* and *B* of plate fig. 1, a well developed columnar epithelium was

found, and since the epidermal cells are more nearly isodiametric in normal sprouts, it was expected that the chemical examination would disclose the presence of enzymes. Such however was not the case. No enzymes were detected, and this experience emphasizes the truth that any inference as to the function of an organ or tissue, based upon structure alone, cannot always be relied upon, unless substantiated by positive evidence.

Further confirmation of the absence of enzymatic action was obtained by examining microscopic sections of the walls of the channels made by the sprouts in the tissue of the tuber. There were no signs of corrosion of the cell walls nor of the starch grains within the cells (plate fig. 2).

Only one alternative remained: the sprouts made their way through the tissue of the tuber by mechanical pressure alone. This conclusion found abundant confirmation. The wall cells of the channels made by the sprouts were greatly compressed by the advancing tip (plate figs. 2 and 4). In light of the studies made on the mode of emergence of lateral roots, it is instructive to compare plate figs. 3 and 4. This latter figure is a detail of the tissues at the point marked *C* in plate fig. 1. Fortunately, at this point a lateral root had begun to develop, and it is clearly seen (fig. 3), not only that the walls of the cortical cells show no signs of enzymatic action, but that they are evidently compressed by the advance of the developing root tip. The paths of the ingrowing sprouts and of emerging lateral roots are evidently made in the same manner, namely by mechanical pressure alone, unaided by enzymatic action.

Experimental production of ingrowing sprouts

But how did the ingrowing sprouts start? Do they, as suggested above, represent normal sprouts that for some unexplained reason turned their tips toward the tuber and penetrated through the skin? There is no evidence for this view. In numerous cases where the "eyes" were deeply indented, small sprouts grew out laterally until their tips came into contact with the skin of the potato. But, as in the case of POND'S attempt to cause one root of *Lupinus* to penetrate another held firmly at right angles to it, so here the surface of the potato was indented by the tip

of the sprout, but no case of penetration was observed. At the writer's suggestion, Miss LUCILE KEENE,[2] then a senior in the University of Missouri, endeavored to secure the penetration of one potato by the sprouts of another. The two tubers were bound tightly together with stout cord, and buried in moist sphagnum. In no case were the sprouts successful in penetrating through the uninjured skin of the adjacent tuber, though the latter was indented. However, if the sprouts were placed against the cut surface of another potato, they entered easily, made their way through the parenchymatous tissue to and *through* the skin at the farther surface. That the sprouts can easily penetrate the cortex from within, though not from without, was shown by the abnormal cases where such penetration was general (fig. 4). Had enzymolysis been a factor, the sprouts might as easily have penetrated from without. The experiments with roots, as noted above, gave analogous results.

The observed facts will not admit of a definite denial of reversal of polarity. Many of my dissections cannot reasonably be interpreted in any other way, but it still seems possible, though not always probable, that the ingrown sprout arose as a lateral branch starting at the very base of the main sprout and *below the skin of the tuber*. This hypothesis at least does not make as large a draught on pure faith as one involving the conception of a reversal of polarity in the shoot. DETMER (**2**) long since called attention to the fact that while the intensity of polarity varied greatly with different species, it was especially well marked in the case of *Solanum tuberosum*.

The cause of tuber-formation

What caused some of the ingrown sprouts to form tubers? The answer to this question is of course bound up with the larger question as to why potato branches ever tuberize. The literature bearing on this problem was discussed by the writer (**3, 4**) in 1906, and need not be reviewed here. Reference may again be made, however, to the suggestion of BERNARD that the formation of tubers is due to a species of *Fusarium*, endotropic with *Solanum tuberosum*.

[2] Miss KEENE also found a similar case of ingrowing sprouts in Montana, but the sprouts were only slightly branched, and formed no tubers within the old potato.

This suggestion was tested experimentally by JUMELLE, but with negative results. Quite evidently this factor does not enter in the tuberization of branches of the ingrown sprouts. GOEBEL cites tuber-formation as an illustration of "qualitative correlation," stating that it is a function of the relation of the branch to the whole shoot system, its underground position, and the material supplied to it.

It seems to the writer that an attempt to explain such a deep-seated character as the formation of tubers by potato plants is like trying to explain the cornness of corn. We may ascertain experimentally what external conditions or combination of circumstances must be realized in order that tubers may result, but that they form at all is because the plant is *Solanum tuberosum*, rather than *Pisum sativum* or *Solanum Dulcamara*. To use a recent and very valuable terminology, the formation of tubers by *Solanum tuberosum*, or by any other tuber-forming species, under suitable environmental conditions, *is an expression of the genotypical constitution of the plant*. Further explanation than this lies far in the future.

Conclusion

1. Ingrowing sprouts of *Solanum tuberosum* make their way through the tissue of the tuber not by enzymatic digestion of a channel in the tissue, but by the mechanical pressure which accompanies growth in length.

2. Potato sprouts do not elongate with force sufficient to penetrate through the uninjured "skin" of the potato tubers from the outside, but they easily penetrate the skin from the inside.

3. A reversal of polarity in ingrowing potato sprouts is not definitely demonstrated, but there is evidence pointing to this conclusion.

4. Tuberization of branches takes place freely on ingrown sprouts of *Solanum tuberosum*.

5. The formation of tubers on *Solanum tuberosum* is a function of external conditions plus the genotypical constitution of the species.

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BROOKLYN BOTANIC GARDEN

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EXPLANATION OF PLATE XXXVI

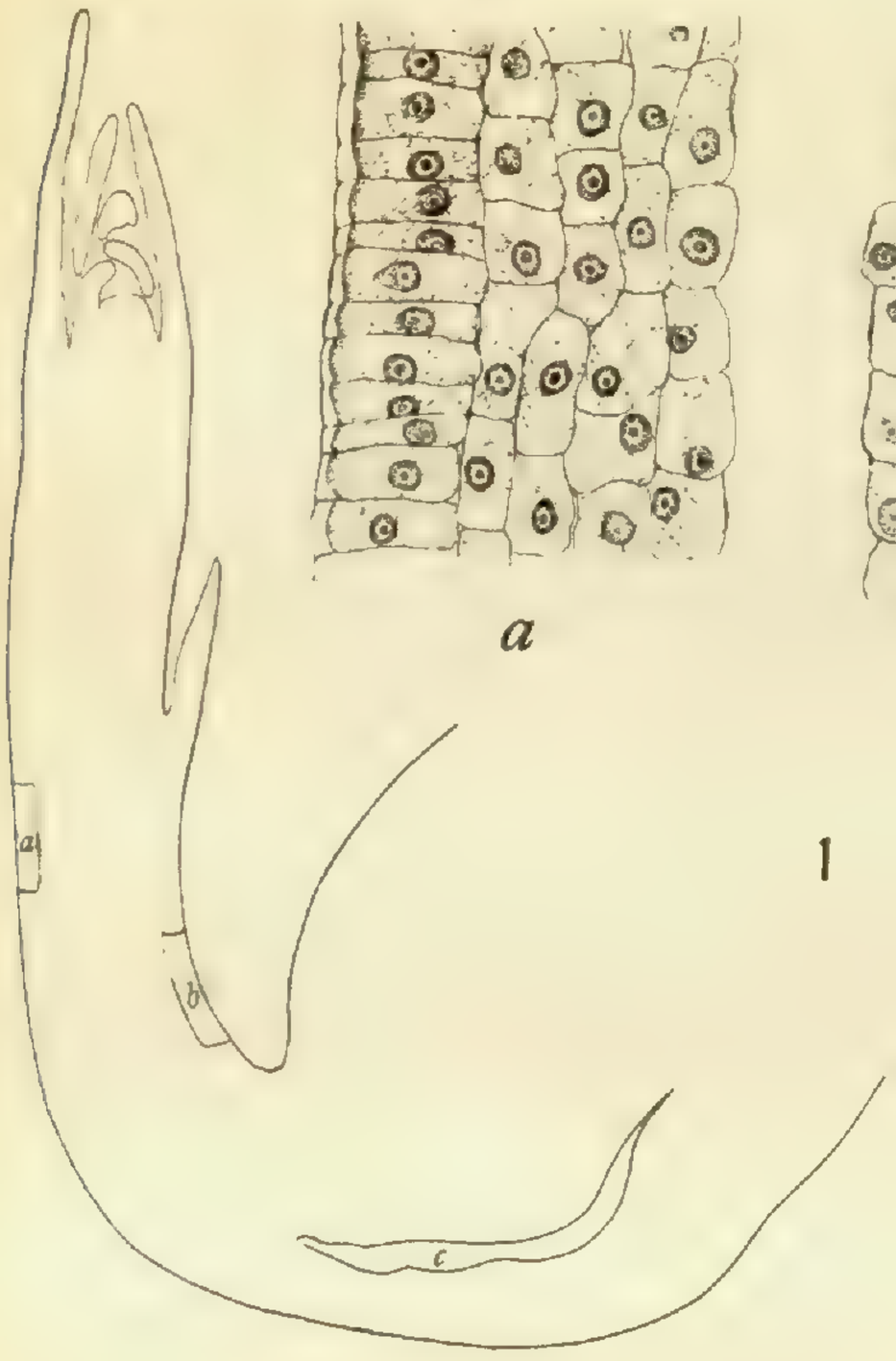
Solanum tuberosum

FIG. 1.—Outline of a longitudinal section of an ingrown sprout: *A* and *B*, cellular structure at the regions marked *A* and *B* in the outline, showing well developed columnar epithelium.—Zeiss oc. 4; obj. D.

FIG. 2.—Longitudinal section through the tip of an ingrown sprout, with adjacent tissue of the seed tuber, showing mechanical compression of the cells of the tuber by the growing sprout and absence of any evidence of corrosion of either cell walls or starch grains; the breaks in the cell walls are artifacts; many of the starch grains have fallen out of the section.—Cf. figs. 3 and 4.—Zeiss oc. 4; obj. AA., lower lens only.

FIG. 3.—Early stage in the development of a root within an ingrown sprout; this section was taken at the area marked *C* in fig. 1; note the compression of the cortical cells by the advancing root.—Cf. figs. 2 and 4.—Zeiss oc. 4; obj. AA.

FIG. 4.—Cross-section through a seed tuber, showing compression of the wall cells of a channel made by an ingrown sprout.—Cf. figs. 2 and 3.—Zeiss oc. 4; obj. AA.



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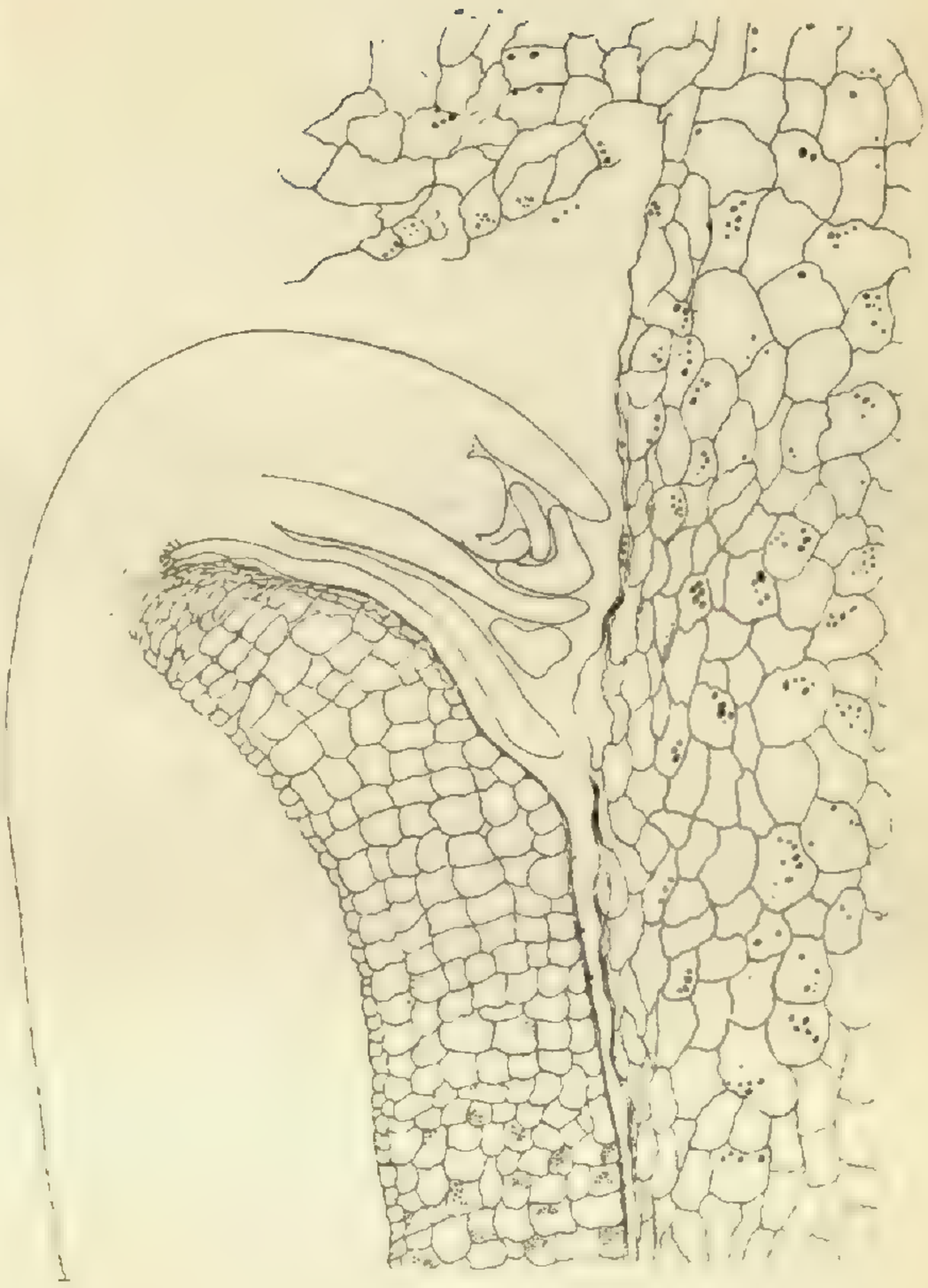

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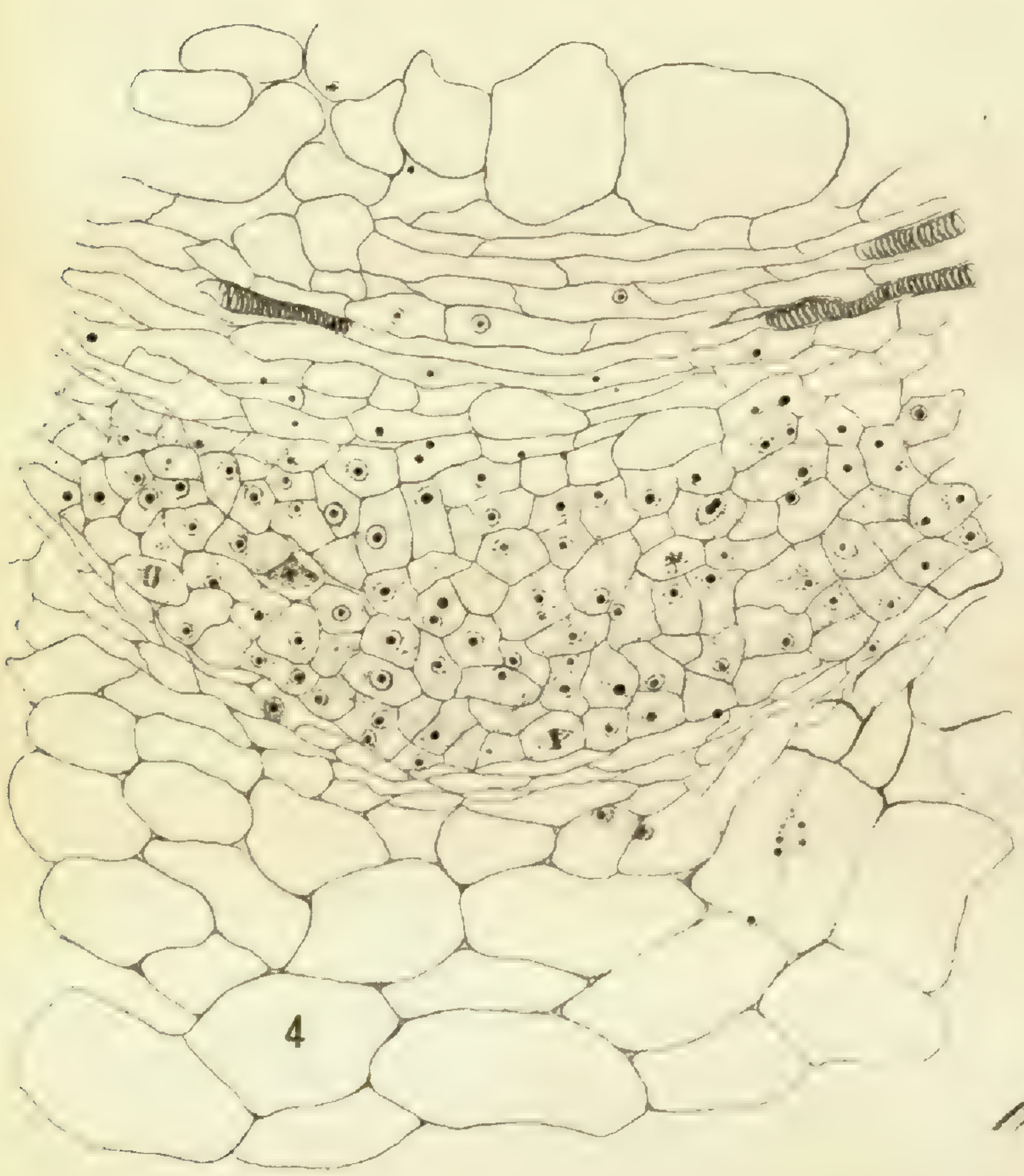

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GAGER on INGROWING SPROUTS

THE ABORTIVE SPIKE OF BOTRYCHIUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 164

O. O. Stoland

(WITH TWENTY-ONE FIGURES)

Interest in the study of the vascular anatomy of the Ophioglossaceae has increased since Chrysler's work[1] on the nature of the fertile spike appeared in 1910. He made the vascular supply of the leaf the basis for concluding that the fertile spike represents two fused basal pinnae. The nature of the vascular supply of the abortive spike has so far received no special attention.

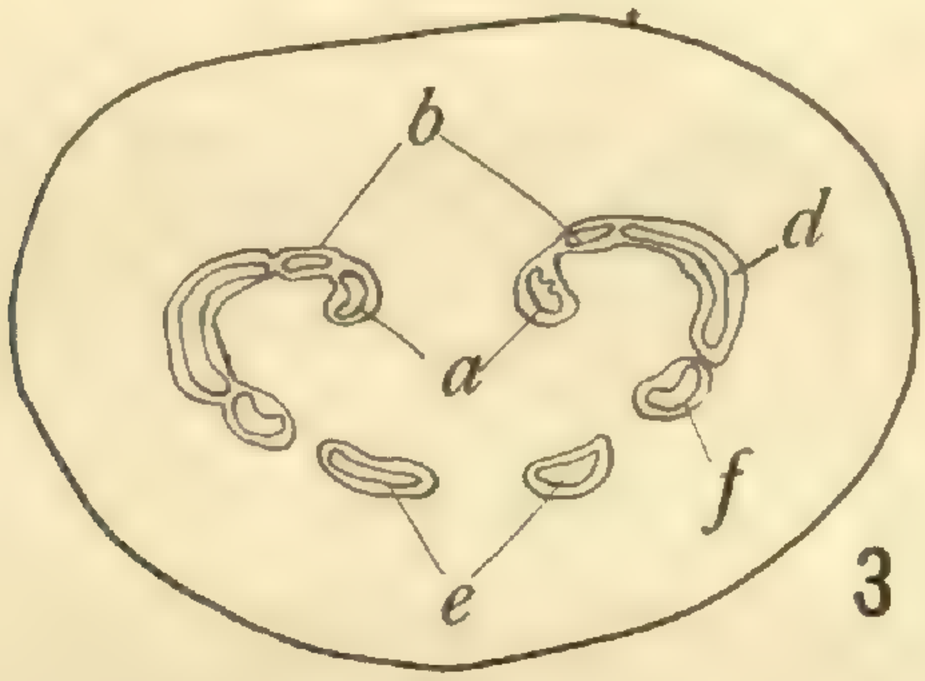
This investigation was undertaken to determine the origin and nature of the vascular supply of the abortive spike, and to compare it with that of the sterile pinnae and the fertile spike. Chrysler found that the series of changes undergone in the origin of the strands to the sterile pinnae were precisely the same as those for the fertile spike.

The material studied was *Botrychium virginianum*, the species from which Chrysler made his figures illustrating the origin of the strands to the fertile spike and sterile pinnae. The abortive spike is of very common occurrence in this species. It appears on the adaxial side of the petiole as a minute structure about 2 cm. below the first pair of sterile pinnae (figs. 1, 2). The fertile spike, however, always comes off from the main axis slightly below the first pair of pinnae. The elongation of the petiole after the abortive spike separates from the axis leaves it some distance below the first pair of pinnae.

Figs. 1, 2.—Fig. 1, adaxial view of the petiole, with the abortive spike and first pair of pinnae cut off; one-half natural size; fig. 2, lateral view of same.

[1] Chrysler, M. A., The nature of the fertile spike in Ophioglossaceae. Ann. Botany 24:1–18. *figs. 1–16. pls. 1, 2.* 1910.

Serial sections were made throughout the petiole from about 8 cm. below the abortive spike to the place where the first pair of sterile pinnae appear. Figs. 3–10 show the changes undergone in



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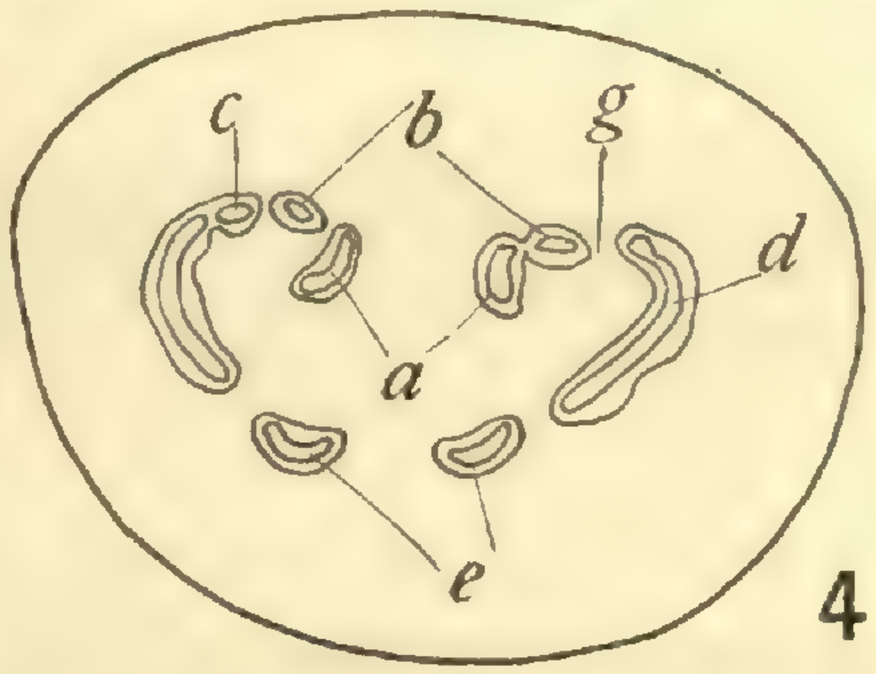

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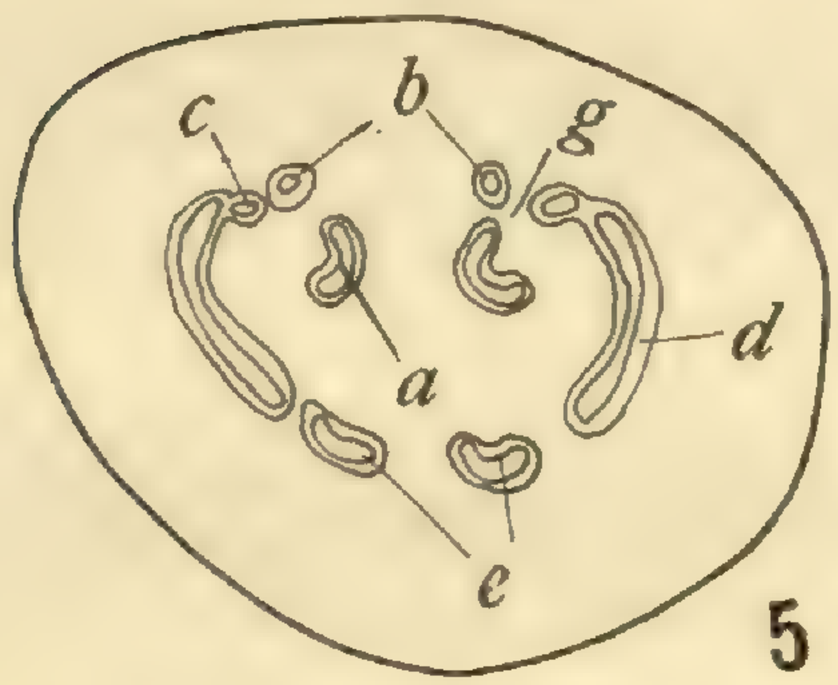

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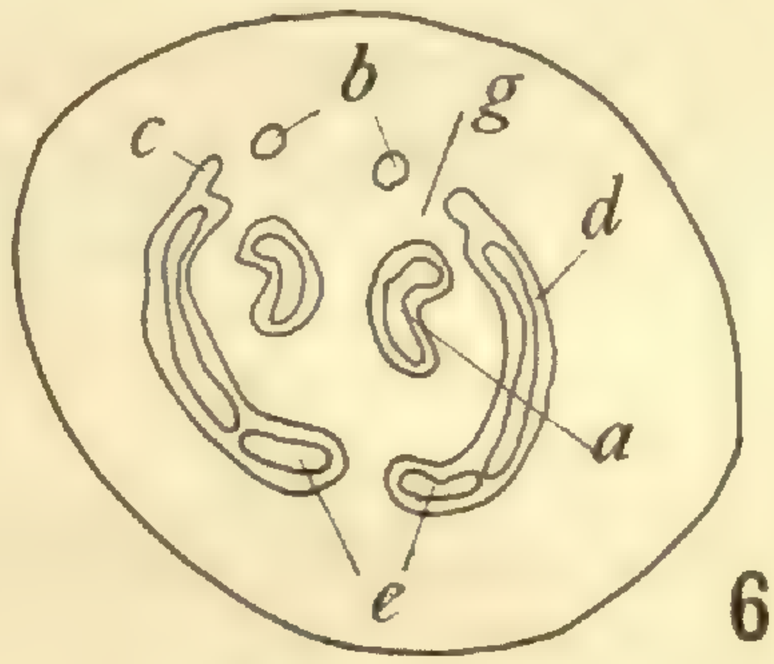

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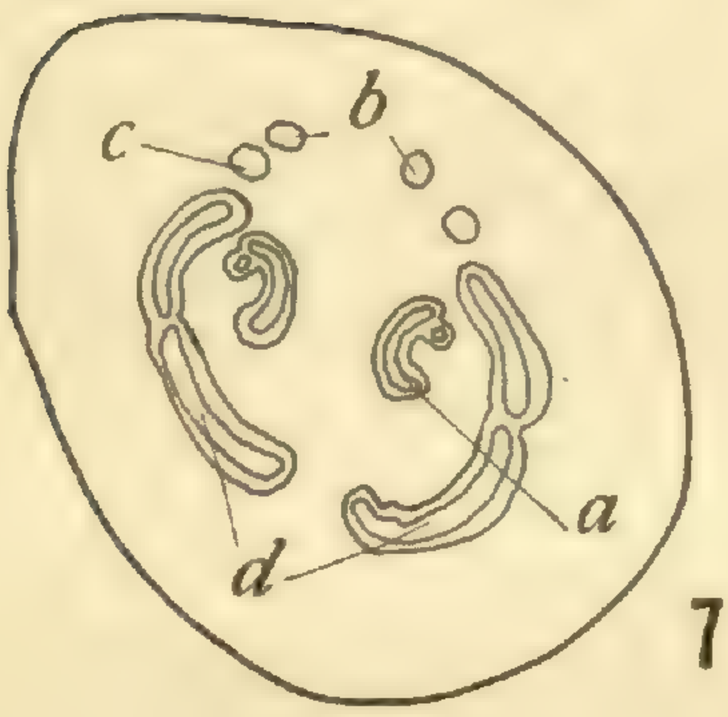

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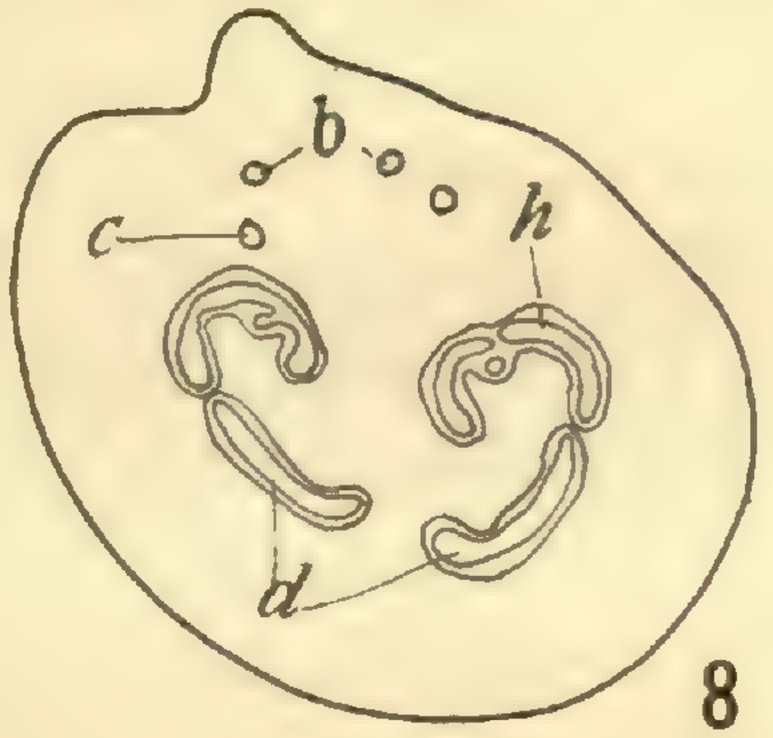

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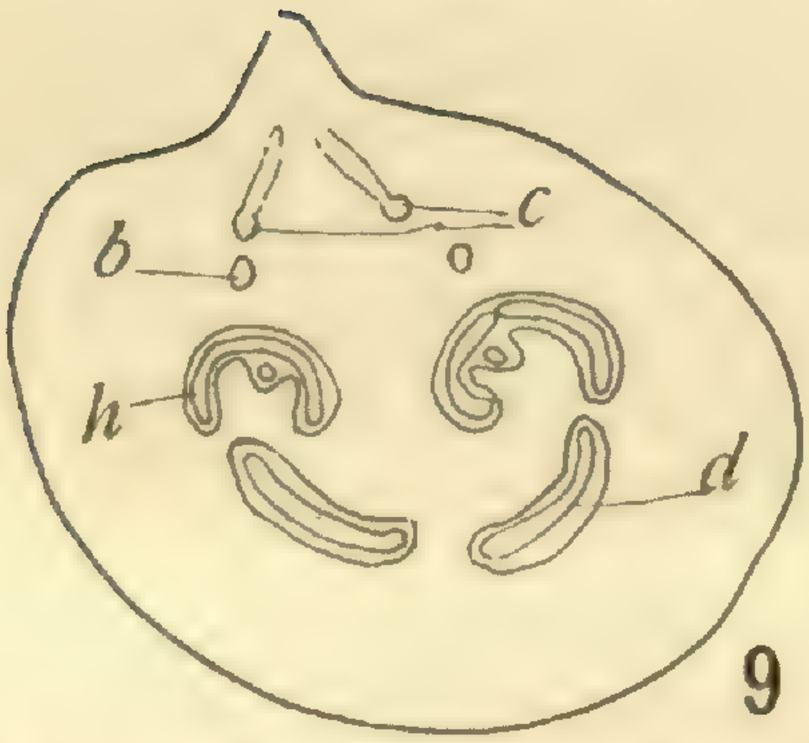

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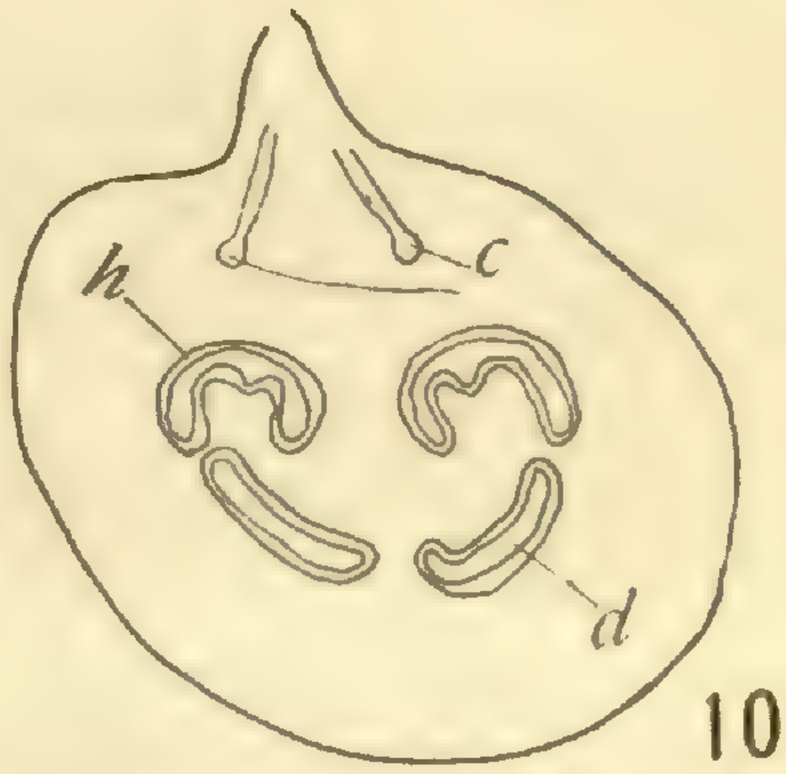

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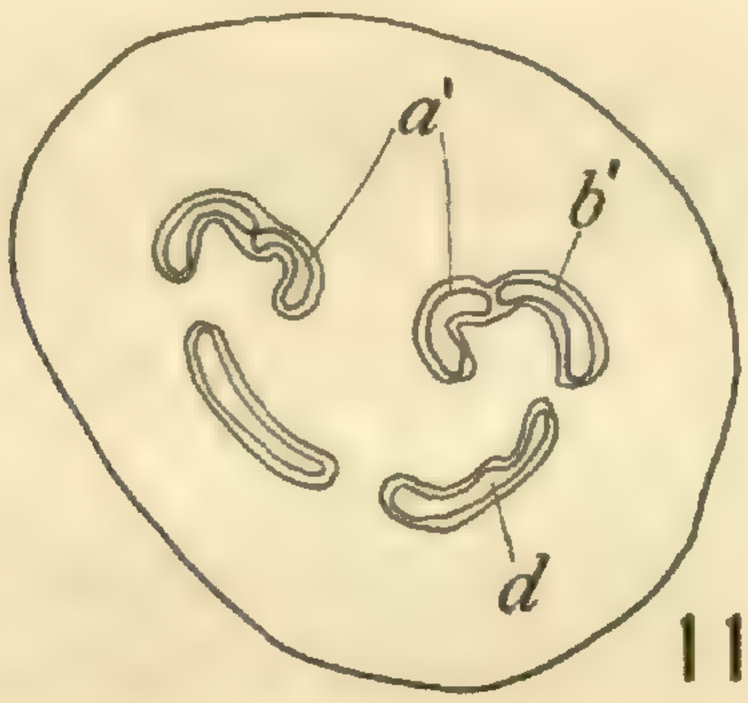
FIGS. 3–10.—Diagrams illustrating the origin of the vascular strands to the abortive spike, made with the aid of an Abbé camera lucida and reduced one-half in reproduction: distances below abortive spike as follows: fig. 3, 7.6 cm.; fig. 4, 5.3 cm.; fig. 5, 2.1 cm.; fig. 6, 4 mm.; figs. 7 and 8, about 1 mm.; figs. 9 and 10, opposite the abortive spike; adaxial side of petiole placed upward; ×15.

the vascular strands relative to the supply of the abortive spike. The vascular strands are all of the concentric type throughout the aerial part. About 8 cm. below the abortive spike the leaf trace consists of three pairs of strands (fig. 3, *d*, *e*, *f*), one large lateral pair (fig. 3, *d*), and two pairs on the abaxial side (fig. 3, *e*, *f*). One of the pairs (fig. 3, *f*) soon unites with the abaxial margin of the lateral strands (fig. 4). The second pair (fig. 3, *e*) remains free to within 1 cm. of the abortive spike, where it also unites with the abaxial margins of the lateral strands (fig. 6). The vascular strands of the abortive spike originate about 8 cm. below the point where the spike leaves the petiole. The adaxial arms of the lateral strands become hooked (fig. 3) and soon a curved strand (figs. 3–7, *a*) is cut off so that a gap is left in the sides of the leaf traces (figs. 4–6, *g*). From each side of these gaps a small strand breaks off to supply the abortive spike (figs. 4–8, *b*, *c*). The outline of these strands appears below the gap, so that they really originate from its base (fig. 3, *b*).

There are then four strands, that is two on each side, that supply the abortive spike. They adhere to the sides of the gap for some distance, but finally break off, one 5 cm. (figs. 4, 5, *b*), the other about 2 cm. (fig. 7, *c*) below the abortive spike. From this point they remain as separate strands running along the gap and finally enter the abortive spike (figs. 9, 10, *b*, *c*). The gaps in the lateral leaf traces close about 4 mm. below the abortive spike (fig. 8). At about this point the two lateral traces (fig. 8, *d*) each divide into two equal strands. The adaxial strands thus formed are hooked (figs. 8–10, *h*). These adaxial hooked strands each divide into two equal parts (fig. 12, A', b') of which the outer pair (b') diverge to pass out to the pinnae (figs. 11–15, b'). Another pair of strands (figs. 13, 14, c') arise from the adaxial margin of the lateral strand (figs. 13, 14, *d*), so that each pinna has two strands. Where these strands (c') leave the leaf trace the gap becomes closed, strand a' uniting with strand *d*. The leaf trace above the origin of the first pair of pinnae consists of two lateral strands (fig. 15, *d*). By a study of figs. 3–15 it will be seen that the same series of changes occurs in the origin of the vascular supply of the sterile pinnae as for the abortive spike.

In some of the leaves examined the vascular supply of the abortive spike consisted of a single pair of strands, that is, one from each side, but in such cases there were two pairs of strands for



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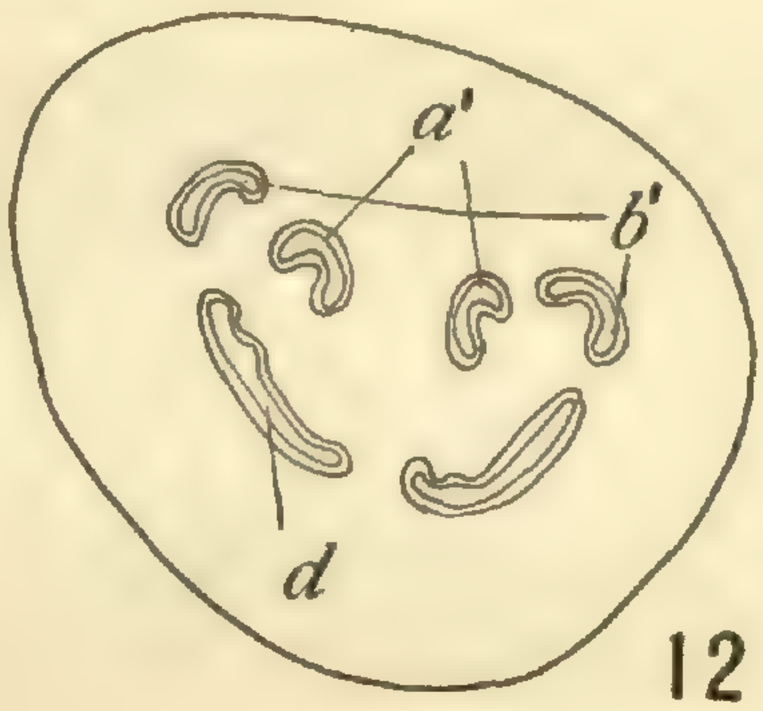

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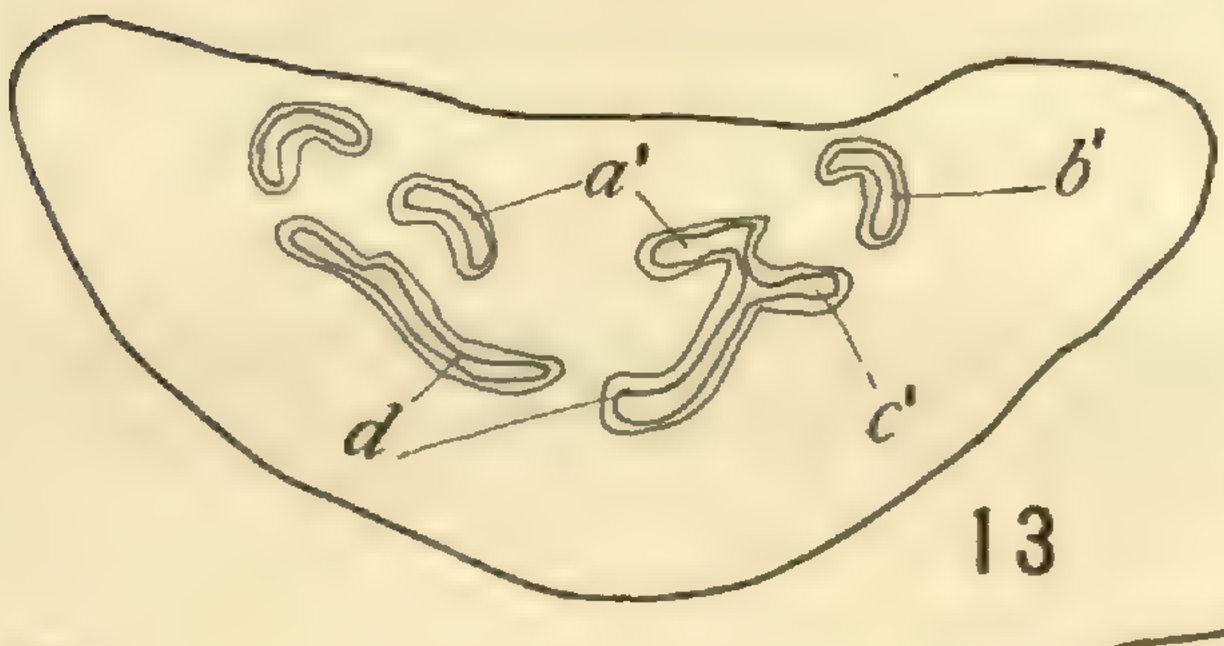

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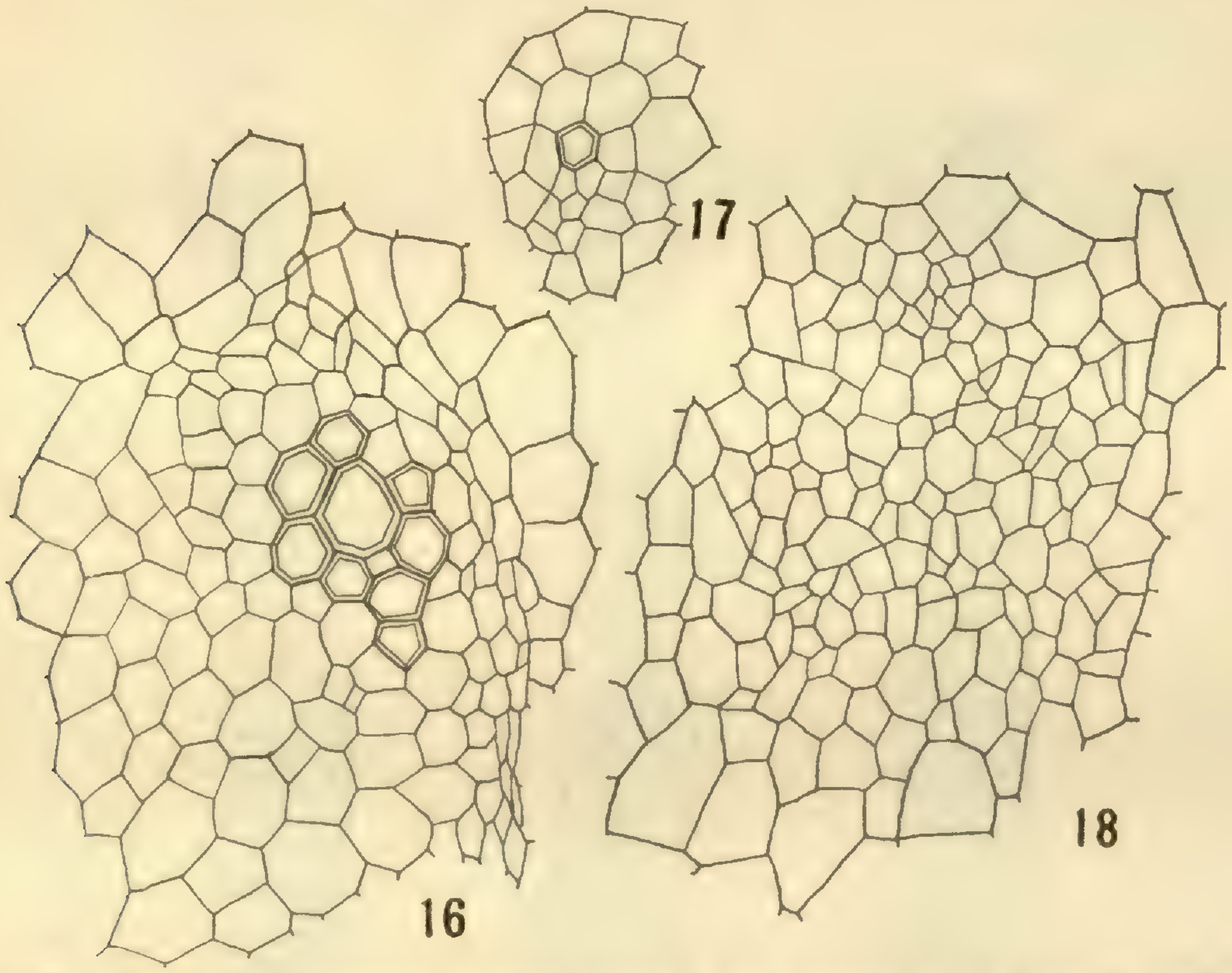
FIGS. 11–15.—Diagrams following the series shown in figs. 3–10, illustrating the origin of strands which supply the first pair of sterile pinnae; fig. 11, 5 mm. above abortive spike; fig. 12, 1 cm. above it; figs. 13–15, opposite the point where the pinnae diverge.

each pair of sterile pinnae. As shown in figs. 16–18, the strands of the abortive spike may have well developed primary xylem in the lower stretches (fig. 16), but farther up the xylem gradually fails to appear (fig. 17), and before they turn outward no xylem is formed. Here the strands are distinguished by their narrow elongated cells. In other cases no traces of xylem could be found throughout strands of the abortive spike.



FIGS. 16–18.—Transverse sections through the strands of the abortive spike, showing development of xylem; fig. 16, 12 mm. below abortive spike; fig. 17, 4 mm.; fig. 18, 3 mm.; ×210.

If figs. 3–15 are compared with CHRYSLER'S figures showing the origin of the strands to the fertile spike, it becomes evident that the changes are essentially the same. A few exceptions may be noted. The first strand (*a* and *a'*) which breaks off on the adaxial side does not unite with the inner face of the large strand as it does in the case of the fertile spike. The gaps left by the strands to the abortive spike are much more evident. These are shown in the photographs of models in figs. 19–21. These models show only one-half of the vascular supply. In fig. 19, which shows the inner

face of the lateral strand, the two strands to the abortive spike are very evident, with the long gap behind them. The gap is seen even better in fig. 20, which shows also part of the adaxial face. Fig. 21 shows the adaxial face of the model with the two narrow strands to the abortive spike obscuring the gap. Four such strands are present in the petiole, but the model shows only one-half of the

19 20 21

FIGS. 19–21.—Photographs of model of the leaf traces on one side of the petiole in region where strands to abortive spike originate; fig. 21, adaxial face.

vascular supply. The pinnae of the leaves bearing the fertile spike usually have only one vascular strand, while those that accompany the abortive spike have two in all cases examined.

The breaking up of the leaf traces into curved rows of bundles below the origin of the strands to the abortive spike does not occur as regularly in the petioles with the fertile spike. This condition is described by CHRYSLER for *Ophioglossum* and *Helminthostachys*,

where the vascular supply of the fertile spike is derived from curved rows of strands.

Summary and conclusions

1. The leaf trace of the petiole bearing the abortive spike consists of several bundles instead of two bundles as usually found in the petiole bearing the fertile spike.

2. The vascular supply of the abortive spike consists of two or four strands arising from the edges or the base of the gap in the leaf trace.

3. The pair of sterile pinnae following the abortive spike are supplied by two pairs of strands originating in the same way as those for the abortive spike.

4. Xylem may or may not appear in the strands to the abortive spike, but it never appears throughout the entire strand.

5. The difference between the origin of the strands to the abortive spike from those to the fertile spike is very slight.

6. The nature of the vascular supply of the abortive spike supports CHRYSLER'S contention that it represents two fused basal pinnae.

This work was undertaken at the suggestion of Professor COULTER and under the direction of Dr. CHAMBERLAIN, and I wish to express my appreciation for their valuable suggestions and criticisms. I also wish to express my thanks to Dr. M. A. CHRYSLER for valuable criticism.

UVIVERSITY OF CHICAGO

PLANTS WHICH REQUIRE SODIUM

W. J. V. Osterhout

(WITH TWO FIGURES)

It has long been customary to regard sodium as necessary for animals but not for plants. In the light of our present knowledge of the rôle of inorganic salts, it is clear that this distinction between plants and animals is of fundamental importance, if it be true in all cases; but if exceptions occur, its significance largely disappears. The experiments which are described here were undertaken in order to learn whether there are cases in which sodium is as necessary for plants as for animals.

One flowering plant was studied, and several genera of algae, among which were representatives of the green, brown, and red algae. The investigation included species from the Atlantic and the Pacific.

The method consisted in replacing the NaCl of the sea water by one of the following substances in turn: NH_4Cl, CsCl, RbCl, LiCl, KCl, $MgCl_2$, $CaCl_2$, $SrCl_2$, $BaCl_2$,[1] $MgSO_4$, and K_2SO_4. After some preliminary experiments it became evident that the best substitutes for Na are Ca, Mg, and K. An attempt was then made to get better results by using these as substitutes for NaCl in the following combinations (the figures refer to molecular proportions as shown in the table): 500 $MgCl_2$+500 $CaCl_2$, 250 $MgCl_2$+750 $CaCl_2$, 500 KCl+500 $CaCl_2$, 667 KCl+333 $CaCl_2$, 910 KCl+91 $CaCl_2$.

All the salts were carefully tested before using and were recrystallized when necessary. The water was twice distilled from glass without the use of rubber or cork stoppers; in place of these a plug of absorbent cotton was employed. The water thus produced was not toxic to such test objects as *Spirogyra* and the root-hairs of *Gypsophila*, and its quality was further shown by the fact

[1] The introduction of $BaCl_2$ and $SrCl_2$ produced precipitates of $BaSO_4$ and $SrSO_4$ which were allowed to remain at the bottom of the dish during the experiment.

that *Phyllospadix* after being transferred directly to it from the sea water lived for 47 days.

All the solutions were made neutral to phenolphthalein before being used. The material was placed in glass dishes in diffused light and kept covered to exclude dust.

The average temperature in experiments with the Pacific species was about 20° C. and was not subject to much fluctuation. In the experiments on the Atlantic coast the jars containing the plants were partly submerged in running water during the entire period of the experiment, and the temperature did not vary far from 20° C.

It is very important to avoid an excessive amount of light. The optimum must be determined in each case by experiment, but is usually less for algae than for flowering plants.

The plants lived much longer in sea water (whether natural or artificial) than in any solution in which the sodium of the sea water was replaced by some other substance. The best substitutes for Na are Ca, Mg, and K. The accompanying table shows the length of life of the plants in solutions made up with these substitutes. It is evident that we cannot say that one of these substitutes is better than another unless we also specify what plant is being experimented on. With one plant Ca fills the place of Na better than anything else, while with another K proves better; with still another Mg is better; and in still other cases combinations (for example, Mg+Ca or K+Ca) are advantageous.

Great diversity was observed among the different species in respect to their behavior toward the other substances which were employed as substitutes for NaCl. To *Phyllospadix* the substitution of Li in place of Na is much more injurious than that of Rb, but just the opposite is true of *Ulva*, while the other plants seem to be injured about as much by Li as by Rb. Similar diversities are found in the behavior of the plants toward the other salts. These facts are important in so far as they give us a clue to the specific action of salts in life processes; this subject will receive further discussion in a subsequent paper.

All the different plants agree in showing that the replacement of Na by Ca, Mg, or K, all of which are present in considerable quan-

tity in sea water, is less injurious than the introduction of such substances as NH_4, Ba, Sr, Cs, Rb, and Li.

Some attempts were made to obtain a better solution by combinations of $MgCl_2+MgSO_4+KCl+CaCl_2$ in the proportions in which they occur in sea water and also in various proportions other than those mentioned above. So far, however, no combi-

TABLE SHOWING DURATION OF LIFE IN DAYS

Culture solution	Phyllospadix Torreyi	Ulva lactuca	Porphyra perforata	Porphyra naiadum	Egregia Menziesii	Nitophyllum multilobum	Chondrus crispus
Tap water	49	23	4	..	4	..	12
Distilled water	47	27	4	..	4	..	8
Sea water	102+	134+	50+	15+	17+	18+	90+
Artificial sea water—							
Stock solution*							
78 cc. $MgCl_2$ .375 M, 38 cc. $MgSO_4$ .375 M, 22 cc. KCl .375 M, 10 cc. $CaCl_2$ .375 M +1000 cc. NaCl .375 M	102+	134+	50+	15+	17+	18+	90+
Stock solution+ 1000 cc. $CaCl_2$ .375 M	56	52	16	3	5	2	12
Stock solution+ 1000 cc. $MgCl_2$ .375 M	52	52	10	2	5	2	30
Stock solution+ 1000 cc. KCl .375 M	73	21	8	1	2	1	12
Stock solution+ 1000 cc. $MgSO_4$ .375 M	47	47	8	$\frac{3}{4}$	2	1	12
Stock solution+ 1000 cc. K_2SO_4 .1875 M	60	21	6	1	2	1	..
Stock solution+ 500 cc. $MgCl_2$ .375 M, 500 cc. $CaCl_2$ .375 M	52	89	10	2	6	2	12
Stock solution+ 250 cc. $MgCl_2$ .375 M, 750 cc. $CaCl_2$ .375 M	52	52	10	2	$4\frac{1}{6}$	2	15
Stock solution+ 500 cc. KCl .375 M, 500 cc. $CaCl_2$ .375 M	47	28	10	1	3	2	17
Stock solution+ 667 cc. KCl .375 M, 333 cc. $CaCl_2$ .375 M	73	21	10	1	3	1	12
Stock solution+ 910 cc. KCl .375 M, 91 cc. $CaCl_2$ .375 M	66	28	6	$\frac{3}{4}$	2	1	8

The (+) sign denotes that the plants were alive when the experiment was discontinued.
* It should be noted that the stock solution contains no NaCl.

nation has been found which is decidedly better than those given in the table.

Similar results were obtained with *Gigartina*, *Ptilota*, *Iridaea*, and *Prionitis*.

Very much more striking results were obtained when experiments on regeneration were made in these solutions. Pieces of

Ulva were cut into strips and placed in the solutions. In sea water and in artificial sea water the cells along the cut edges grew and divided repeatedly, but this did not occur in any of the solutions which lacked sodium (figs. 1 and 2).

In view of these results we may conclude that for the plants studied sodium is as necessary as for animals. That its function is not merely to maintain osmotic pressure is evident from the fact that if sodium chloride be replaced by an osmotically equivalent amount of cane sugar the plants quickly die. That sodium is

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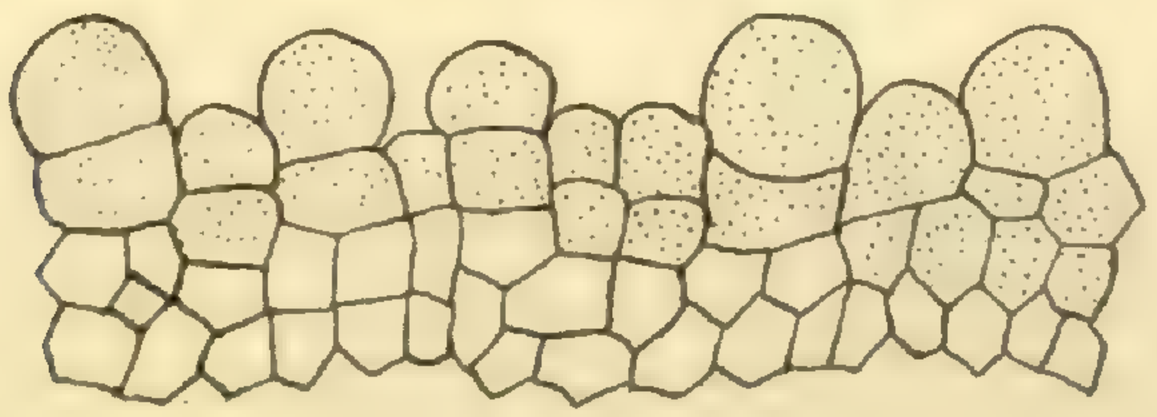

2

FIGS. 1 and 2.—Fig. 1, portion of a frond of *Ulva* cut along one edge for experiments on regeneration; fig. 2, regeneration along the cut edge of a frond of *Ulva;* the newly formed cells are dotted; this regeneration takes place only in solutions containing sodium.

needed to antagonize the toxic action of the other salts in the solution is clear from these and previous experiments.[2] Whether sodium is needed for nutrient purposes must be decided by further experiments.

Since this investigation was begun, papers by RICHTER[3] have appeared in which he states that sodium is necessary for the nutrition of certain marine diatoms but not for that of other marine algae. Aside from diatoms his experiments seem to have been confined to a single unicellular alga. Many unicellular forms are so exceptional in their behavior that it would be unwise to draw general conclusions from experiments conducted on them alone. RICHTER states that while they grow in the absence of NaCl, they

[2] OSTERHOUT, BOT. GAZ. **42**:127. 1906.

[3] RICHTER, Sitzungsb. Kais. Akad. Wien **118**:1337. 1909.

grow much better when it is present. In his experiments only Na, K, Mg, and Ca were used, and the proportions employed were not those which exist in sea water.

Summary

Sodium is as necessary for the marine plants studied as for animals; its replacement in sea water by NH_4, Ca, Mg, K, Ba, Sr, Cs, Rb, or Li is decidedly injurious.

The best substitutes for Na are the other kations which predominate in the sea water, Mg, Ca, and K.

The behavior of various species toward certain salts indicates that each of these salts has a specific action on life processes.

LABORATORY OF PLANT PHYSIOLOGY
HARVARD UNIVERSITY

BRIEFER ARTICLES

THE PERFECT STAGE OF THE ASCOCHYTA ON THE HAIRY VETCH

It is quite well known that species of the form-genus *Ascochyta* produce a disease of the vetch, pea, and other leguminous plants. In the autumn of 1908 I collected a number of affected pods of the hairy vetch (*Vicia villosa*) which was growing on the farm of Cornell University. These were placed in a wire cage and partly covered by some leaves and grass used as a mulch for *Rhododendron maximum* in my garden. It was hoped that the perfect stage might be obtained. During early May in 1909 the cage was taken to the laboratory, and a few pods were found on which there were a number of perithecia which proved to belong to the genus *Sphaerella* (*Mycosphaerella*), although pycnidia of the *Ascochyta* were present on the same pods. They were at some distance from the perithecia, and by using care it was not a difficult matter to obtain an abundance of ascospores for making pure cultures in bean pod agar, and also for inoculation of vetch seedlings.

The germination of the ascospores was studied and the growth of the colonies was observed up to the formation of pycnidia and pycnospores identical with those formed on the vetch pods, evidence that this *Sphaerella* was the perfect stage of the *Ascochyta* of the vetch. Inoculations of vetch seedlings were made with pycnospores obtained in pure culture from sowings of ascospores. These were somewhat slow in taking, but on May 18 a few brown spots appeared on the stems, and on May 24 some of the leaves were dead and pycnidia of the *Ascochyta* were present.

On May 13 ascospores taken directly from the pods of the vetch were sown on vetch seedlings. On May 17 brownish depressed spots were present on the stems. By May 18 these spots had encircled the stem and the terminal shoot was thus killed. Again on May 15 ascospores were placed on young vetch seedlings. On May 18 a few of the leaves were dead and pycnidia were present. By May 22 the disease had spread somewhat and more pycnidia of the *Ascochyta* were formed. On May 15 pea seedlings about 10 cm. high were inoculated with asco-

spores from the vetch pods. By May 18 the edges of some of the leaves were dead and a few pycnidia of *Ascochyta* were formed. In all of these cases check host plants remained free from the disease.

The ascospores are shot out from the asci on the absorption of water. This was observed in a number of cases. While this is given as the characteristic method of escape of spores in the family Mycosphaerellaceae, the behavior of the asci and spores is not the same in all species. In this *Sphaerella* the outer, firm layer of the ascus wall is ruptured or dissolved at the apex, and the inner, thin layer then stretches out to three or four times the length of the mature ascus. When the spores are shot out through the end of this inner membrane, either successively or in a group, the inner membrane, which is very thin, collapses, while the outer layer of the wall, which does not stretch, usually remains firm.

Ascochyta occurs, usually in abundance, on the vetch, pea, and *Melilotus* in the vicinity of Ithaca. For the purpose of comparing the species on these different hosts, studying the life history and interrelationships on the different hosts, this problem was assigned in 1910 to Mr. R. E. STONE, a graduate assistant in the department of botany. This work is now completed and will shortly be published in the *Annales Mycologici*.—GEORGE F. ATKINSON, *Cornell University, Ithaca, N.Y.*

GAUTIERIA IN THE EASTERN UNITED STATES

For many years before seeing a specimen of the genus *Gautieria* I had longed to find one, since it occupies a rather unique position in the Gasteromycetes, because it is the only representative of the group in which a peridium is wanting. From the literature and illustrations I had a fairly good concept of it, and each year wished that I might have a specimen to exhibit to my classes, because it offers such an excellent demonstration of the gleba of a gasteromycete without sectioning or removing the peridium.

On October 30, 1905, Dr. A. A. ALLEN, recently an assistant in the department of zoology at Cornell University, who was then a Freshman, brought into my laboratory a small plant about the size of a marble which I at once recognized as *Gautieria*. He had collected it the previous day while on a stroll through the woods on South Hill about three miles distant from the university. Seeing an old, half-decayed specimen of *Ganoderma applanatum* lying on the ground, where it had fallen from

the trunk of a dead tree, he kicked it over and the specimen of *Gautieria* rolled out from beneath.

A few days later I organized a party of advanced students for an excursion to the locality. In the leaf mold near the dead tree we found some half-dozen other specimens. Specimens have again been found during the past summer by Mr. H. H. FITZPATRICK, one of my graduate students, who has just completed a study of its development, since he found it in all stages of growth.

Gautieria morchelliformis Vitt., of Europe, has been reported from Mexico. *G. monticola* Harkness has been described from California. The species collected in the vicinity of Ithaca I have regarded as *Gautieria graveolens* Vitt., of Europe. It has a strong, peculiar, and unpleasant odor which is characteristic of several closely related species.

The plant is attached at the base to a slender whitish rhizomorph which broadens out within the gleba in the form of anastomosing planes forming the sterile avenues which are covered with the hymenium. These make up the gleba tissue, or walls, which separate the winding chambers which open to the outside. The spores are beautifully sculptured, being longitudinally or obliquely ribbed.—GEORGE F. ATKINSON, *Cornell University, Ithaca, N.Y.*

CURRENT LITERATURE

MINOR NOTICES

Nathanson's textbook of botany.—This book[1] is written from a strictly physiological standpoint, structures receiving scant attention except as they are related to functions. The subject-matter is divided into two parts, the vegetative life and the reproduction. The first part is subdivided into (1) nutrition as a fundamental function of vegetative life, (2) the vegetative organs of the algae, (3) the structural plan of the organs of the higher plants, (4) the life history of the vegetative organs of the higher plants, (5) the orientation of the vegetative organs in space, and (6) the structure of the vegetative organs under special conditions of nutrition. The second part is subdivided into (1) reproduction in the lower plants, (2) mosses and cryptogams, (3) reproduction in flowering plants, (4) the relation between the vegetative life and reproduction, and (5) heredity. The book closes with a few remarks on the principal groups of plants.

This presentation could be read, with profit, by all classes of botanists, particularly by morphologists, who stand in greater need of such a presentation. Morphologists, however, can hardly regard the text as a "general botany," since it gives so little attention to development and phylogeny.—CHARLES J. CHAMBERLAIN.

Natal plants.[2]—The recent appearance of part 4 completes the sixth volume of this well known work. The present part contains descriptions and full-page illustrations of 25 species, most of which are of comparatively recent publication, hence little known. A brief chapter is added giving notes and corrections on plants mentioned in volumes I–VI inclusive. One species, *Brachystelma Franksiae* N. E. Brown, is new to science.—J. M. GREENMAN.

NOTES FOR STUDENTS

Physiology of lichens.—The greatest advantage to the lichen of parasitism with the alga was formerly supposed to be that the lichen received carbon which the alga obtained from the air. But now it appears reasonable to suppose that the lichen may furnish the alga a portion of the carbohydrates which it secures from the substratum. This of course cannot occur when the lichen

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[1] NATHANSON, A., Allgemeine Botanik. 8vo. pp. viii+471. *figs. 394.* Leipzig: Quelle und Meyer. 1912. *M* 10.

[2] WOOD, J. MEDLEY, Natal Plants. Vol. **6,** p. 4, *pls. 576–600.* Bennett & Davis. Durban, 1912.

grows on rocks that contain no organic matter. Breathing pores have been postulated for the lichens in a general way, but we really know little about provision for exchange of gases in these plants. The student will find a general summary by FÜNFSTÜCK in ENGLER and PRANTL'S *Natürlichen Pflanzenfamilien*. In 1906 ZOFP[3] described a new *Ramalina* (*R. kullensis*) which has the so-called breathing pores well developed, and ROSENDAHL[4] in 1907 found them in *Parmelia aspidota*. Nothing more seems to have been added to FÜNFSTÜCK'S statement, and it appears probable that passages from the exterior to the interior of lichen thalli are rare instead of common.

TOBLER[5] thinks that such passages may be expected in thalli with thick cortices, but scarcely in those with thin cortices, where sufficient aeration may occur without them. He believes that the lack of sufficient air and light within the lichen thallus makes the conditions unfavorable for the alga and that this accounts for the layering of the algae near the surface of the thallus. TOBLER cultivated *Xanthoria parietina* and a number of other lichens without algae in a gelatin-beerwort medium and got a rich production of calcium oxalate. He then cultivated the thalli with the algae and was not able to find the oxalate. He supposes, therefore, that the algae used the surplus extracted from the medium by the lichen, and that the same occurs in nature, the lichen taking the oxalate from the organic substratum. We may add that according to ELENKIN'S[6] theory of endosaprophytism, the lichen may extract organic compounds from the dead algae for the living.

TREBOUX[7] is cited by TOBLER to the effect that species of *Chlorella*, *Pleurococcus*, *Cystococcus*, and some other algae investigated, are able to obtain carbon in a very different manner from that known in higher green plants. It was found that these algae are able to thrive on artificial media containing organic acids, and the conclusion was reached that they behave much like fungi with respect to carbon assimilation.

TOBLER failed to notice the excellent work of ARTARI,[8] performed on algae which grow in lichen thalli, to ascertain the physiological relationship of the

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[3] ZOFP, W., Biologische und morphologische Beobachtungen über Flechten. II. Ber. Deutsch. Bot. Gesells. **24**:574–580. *pl. 23*. 1906.

[4] ROSENDAHL, F., Vergleichende anatomische Untersuchungen über die braunen Parmelien. Nov. Act. Kais. Leop. Karol. Akad. **87**:404–459. *pls. 25–28*. 1907.

[5] TOBLER, F., Zur Ernährungsphysiologie der Flechten. Ber. Deutsch. Bot. Gesells. **29**:3–12. 1911.

[6] ELENKIN, A., Zur Frage der Theorie des Endosaprophytmus bei Flechten. Bull. Soc. Imp. Nat. Moscou II. **18**:164–186. 1904.

[7] TREBOUX, O., Organische Säuren als Kohlenstoffquelle bei Algen. Ber. Deutsch. Bot. Gesells. **23**:432. 1905.

[8] ARTARI, A., Über die Entwickelung der grünen Algen unter Ausschluss der Bedingungen der Kohlensäure Assimilation. Bull. Soc. Imp. Nat. Moscou II. **23**:39–47. *figs. 2*. 1899.

algae to the lichens. ARTARI grew *Cystococcus humicola*, obtained from the thalli of *Xanthoria parietina* and *Gasparrinia murorum*, in pure cultures on complicated media containing mineral salts or organic compounds, or in some instances both the salts and the organic matter. He found that the algae grew luxuriantly on the media containing organic matter and were dark green in color when grown in absolute darkness or in light with CO_2 excluded. On media containing mineral salts but no organic matter, the algae grew under similar conditions, but not so well. These results square beautifully with those of TOBLER, the one worker giving special attention to the lichen, and the other to the alga which lives in the thallus of the same lichen. The two researches show conclusively that the alga which lives in the thallus of *Xanthoria parietina* can obtain its organic matter as well as the mineral salts from the lichen, provided the latter grows on some other substratum than rocks that contain no organic matter.

BEYERINCK, BOUILHAC, ETARD, KLEBS, and others have obtained results with algae somewhat similar to those of TREBOUX and ARTARI, two of the authors working on a blue-green alga (*Nostoc*). *Trentepohlia umbrina* grows in the bark of trees, sometimes with lichen thalli and sometimes alone. In fact this alga bores into the bark of trees or effects an entrance through minute openings in the periderm, probably either because abundant light is not favorable to its best development, or because closer relationship with the organic matter of the periderm is more essential to its development than bright light. This alga would be an especially favorable object for such investigations as those noted above.

TOBLER also started cultures of *Xanthoria* on gelatin and transferred them to a liquid medium which contained none of the carbon compounds needed by the alga except what was in the air, and the lichen grew somewhat. The alga grew in the same liquid medium and was of normal appearance. In transferring the lichen, particles of the gelatin were unavoidably carried over. After these were probably consumed by the lichen, the alga was introduced into the culture with the lichen and grew well, but was colorless. This, he thinks, indicates that the lichen had assimilated the acid which the alga needed as a source of carbon, probably oxalic acid. He says that gelatin is not a source of carbon for the alga, so that his conclusions would not be invalidated even if the lichen had not extracted all of the gelatin from the medium before the alga was introduced.

The lichen hyphae soon entwine some of the algal cells in the culture, and thus the parasitic, or at least a symbiotic, relationship is established. TOBLER believes that the lichen obtains carbon from the alga, while the latter replaces it by extracting carbon from the oxalic acid contained in the tissues of the lichen. This means a mutual exchange of food materials between the lichen and the alga, at least as a probability. His investigation seems to indicate that the alga growing in *Xanthoria parietina* and those found in several other lichens very probably obtain their carbon from the lichen, the latter in turn

obtaining it from the organic material in the substratum. This is probably true except for lichens that grow in substrata containing no organic material and perhaps for those having thin cortices. ROSENDAHL found that thinness of cortex and presence of calcium oxalate go together in the species of *Parmelia* studied. This would indicate that the algae in lichens with thin cortices obtain their carbon from the air, and so the oxalate is stored in the lichen, while in the lichens with thick cortices the alga secures little or no carbon from the air and utilizes the oxalate obtained from the substratum by the lichen.

These investigations of TOBLER, ARTARI, and others prove that we know little regarding the nutrition of lichens and their algal hosts. The results already obtained are important and suggestive. It is to be hoped that much more work of this kind may be done.—BRUCE FINK.

Metabolism of fats.—IVANOW has published a series of papers on the metabolism of fats in higher plants. He emphasizes how little our knowledge has advanced in this field since the classical work of SACHS, and contrasts it with the advances made in our knowledge of protein metabolism in plants. IVANOW[9] believes he has established that the synthesis of fats from glycerin and fatty acids comes about through the reversible action of lipase, a view apparently well established in animal metabolism.

Another paper[10] deals with the transformation of fats during germination. In order to have seeds with the greatest possible variation in the nature of the fats as regards the saturation of the fatty acids involved, he used flax (very rich in fatty acids of the linoleic type: $C_nH_{2n-6}O_2$), hemp (rich in the linoleic type: $C_nH_{2n-4}O_2$), rape (rich in the oleic type: $C_nH_{2n-2}O_2$), and poppy (rich in the palmitic type: $C_nH_{2n}O_2$). In the developing seedling he finds that the intensity of consumption of the fatty acids originating from the fats is inversely proportional to the degree of saturation. The linoleic type of acid disappears first, and with it of course the hexabromide test; then follows the linoleic, oleic, and finally the palmitic types. The fall in the iodine number of the fat during germination is due to the more rapid transformation of the more unsaturated acids to carbohydrates, and not to their saturation by oxidation leading to the formation of acids with shorter chains. The acid number of the fat from each plant is a strictly determined matter, low when the fats are rich in unsaturated acids, and high when rich in saturated acids. If the constituent parts of the oil in a plant are known, one can approximate closely the acid number of that oil. The unsaturated fatty acids are largely tied up in the glyceride, while the saturated acids exist to a larger degree in the free state. The transformation of the oils during germination is by

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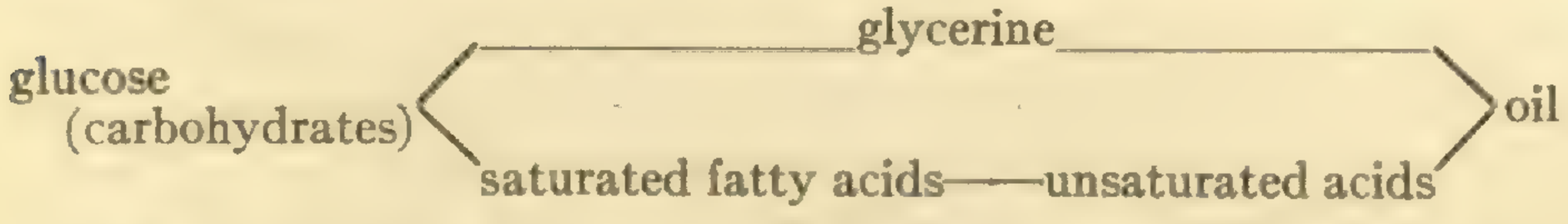
[9] IVANOW, SERGIUS, Über Oelsynthese unter Vermittlung der pflanzlichen Lipase. Ber. Deutsch. Bot. Gesells. **29**:595–602. *fig. 1*. 1911.

[10] ———, Über die Verwandlung des Oels in der Pflanze. Jahrb. Wiss. Bot. **50**:375–386. 1912.

oxidation to carbohydrates, but the intermediate products are not known and are the next substances for investigation. Since the unsaturated fatty acids are so readily oxidized to carbohydrates (an exothermic process) during germination, the author concludes that their appearance in a plant is a special adaptation, making rapid germination possible by a great liberation of energy. As long as we know so little about the phsyiological use, if any, made of most of the energy liberated by such oxidations, this conclusion is without evidence in its favor.

A third paper[11] deals with the synthesis of fats in oily seeds. In the flax, rape, etc., the testa is formed first, followed by the development of the embryo. Pentosans accumulate early, having their only rôle in the formation of protective structures in the testa and playing no part in nutrition. The carbohydrates (glucose, cane sugar, and starch) are the main substances from which fats are synthesized; while the proteins play a minor if any part in the process. Of the carbohydrates, glucose is first used, followed by the hydrolysis and use of cane sugar, and finally starch. Intense oil formation occupies about two weeks in the middle of the seed development period. Up to the time of the beginning of oil formation, carbohydrates are stored in the stem. At this time the hydrolysis of the carbohydrates in the stem begins, and, due to their transformation to insoluble materials, oils, etc., in the seed, a falling gradient is established in that direction, causing the diffusion to the developing embryo. The first acids formed are saturated, as shown by the iodine number. The author also believes that they belong to the higher members of their respective series, for the Reichert-Meissel number is constant, and it does not vary with the acid number. It is also concluded that the volatile acids play no part in fat synthesis. The acid number varies greatly in the oil from various plants, being very low in oils from seeds rich in unsaturated acids. The author believes the following scheme shows the main features of oil synthesis in a form like the flax seed.



The variation in the iodine number with stages of development is the greater the greater the proportion of the unsaturated acids in the oil. In seeds with few fatty acid components in their oils (rape and hemp) the variation in the physical and chemical characters of the oil with stages of development is slight; while in seeds with oils of many fatty acid constituents (flax and poppy) these variations are great.

It must be remembered that such quantitative analyses cannot certainly determine the series of products and reactions involved in a synthesis, for many

[11] IVANOW, SERGIUS, Über den Stoffwechsel beim Reifen ölhaltiger Samen mit besonderer Berücksichtigung der Oelbildungsprozesse. Beih. Bot. Centralbl. **28**: 159–191. 1912.

of the intermediate products may exist in such small quantities as to escape detection.—WILLIAM CROCKER.

Endogone.—A paper by BUCHOLTZ[12] on the subterranean genus *Endogone* presents an unusually important addition to our knowledge of the group Hemiasci, established by BREFELD to include supposed transitional forms between the Phycomycetes and Ascomycetes. Further study of the forms which were originally placed in the Hemiasci has resulted in the gradual dismemberment of that group until it has lost its taxonomic status. As a result of the work of BUCHOLTZ on *Endogone*, that form also must be removed from the Hemiasci and classed with the Phycomycetes. BUCHOLTZ includes in his account 7 of the 17 species of *Endogone* (including one described as new in his paper). Two of these, *E. lactiflua* Berk. and *E. Ludwigii* Bucholtz, have a sexual process resembling that of the Phycomycetes; *E. macrocarpa* Tul. and *E. microcarpa* Tul. produce only chlamydospores; in *E. pisiformis* Link. the zygospores or chlamydospores of the other forms are represented by sporangia whose contents break up into spores as in the mucors; and in the remaining forms studied, *E. lignicola* Pat. and *E. fulva* (Berk.), the mode of reproduction is not definite. In these either sporangia or thin-walled chlamydospores are produced.

The youngest fruit bodies of *Endogone lactiflua* examined consist of a tissue of interwoven hyphae covered by an outer more firmly interwoven layer, forming a sort of peridium. Foreign hyphae occasionally penetrate the fruit body, but these are easily distinguished from hyphae of *Endogone* by their straight course and parallel walls. The hyphae of *Endogone* are sinuous in their course and have many irregular inflations. Male and female gametangia arise as saclike outgrowths of the hyphae. The nuclei in the gametangia are arranged peripherally and undergo one division. There is no differentiation of the protoplasm into periplasm and ooplasm as in the Peronosporales. A large nucleus, whose origin is not clear, appears in the center of the gametangium. The other nuclei pass toward the base of the gametangium, which is then cut off from the upper uninucleate portion by a wall. The process is the same in both gametangia. The fusion of the uninucleate gametes begins at the time of the formation of the wall. The nucleus of one gamete passes into the other gamete, but no fusion of nuclei takes place. At the apex of the fusion cell, now containing both nuclei, a portion of the wall is gelatinized, and at this point a papillate outgrowth appears, which gradually enlarges as the protoplasm and nuclei pass into it from the fusion cell. This outgrowth

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[12] BUCHOLTZ, F., Beiträge zur Kenntnis der Gattung *Endogone* Link. Beih. Bot. Centralbl. **29**: 147–225. *pls. 8.* 1912. Originally published in Russian: Neue Beitr. zur Morph. und Cytologie der unterirdischen Pilze. T. I. Die Gattung *Endogone* aus d. Nat.-Hist. Museum d. Gräfin K. Scheremetjeff in Michailowskoje. Moskau **9**: 1911. See also preliminary note: Über die Befruchtung von *Endogone lactiflua* Berk. Ann. Myc. **9**: 329–330. 1911.

enlarges and forms the zygote or zygospore. The zygospore becomes surrounded by a thick wall showing differentiation into several layers. In its completed state it is inclosed in a network of hyphae whose walls fuse and become greatly thickened, forming, in cross-section, a sort of a corona around the zygospore. The nuclei were not observed to fuse in the zygospore of this species, but in *Endogone Ludwigii* a single large nucleus, supposed to be a fusion nucleus, was observed in some of the zygospores. This process of zygospore formation was observed only in the two species mentioned. In the other species the fruit body is filled with asexually formed chlamydospores or with sporangia in place of zygospores.

In his discussion the author points out the close resemblance between the sexual reproduction of *Endogone* and the mucors on the one hand, and on the other hand certain homologies between *Endogone* and the Ascomycetes. Thus in the peculiar outgrowth of the fusion cell and the paired nuclei, he sees a homologue of the ascogenous hyphae of the Ascomycetes, in some of which (as CLAUSSEN has shown for *Pyronema confluens*) the male and female nuclei do not fuse, but remain in pairs until the formation of the ascus.—H. HASSELBRING.

Position of Gnetales.—In 1911 LIGNIER and TISON published a brief statement of their view that Gnetales are apetalous angiosperms, a statement that was noted and commented upon in this journal.[13] Now they have begun the publication of an extended argument for their position, the first part dealing with *Welwitschia*.[14] A very full résumé of the literature prepares the way for a consideration of all the kinds of testimony available. The conclusions reached cannot be attacked on the basis of insufficient knowledge of the facts at hand, but of course they rest upon personal judgment as to the relative importance of the testimony, as do all conclusions in reference to phylogeny.

The general contention in reference to *Welwitschia* is that the two kinds of strobili ("inflorescences") have identical organization; that in the axil of each bract there occurs a flower of the angiosperm type, comprising five cycles of members; that the two innermost cycles form a tetracarpellary closed ovary prolonged into a long style; that the functionally monosporangiate flowers are obviously derived from more primitive bisporangiate flowers; that *Welwitschia* has retained a large number of gymnosperm characters, especially in its "anatomy and histology"; that in evolution such recondite characters change least rapidly, and therefore the phylogenetic position is to be determined by the floral characters, which are essentially angiospermous; that the great reduction of flowers and their aggregation into inflorescences do not suggest angiosperms in general, but rather a very specialized lateral phylum; that the method of specialization resembles that of the *Amentales*, and therefore *Wel-*

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[13] BOT. GAZ. **51**:479. 1911.

[14] LIGNIER, O., et TISON, A., Les Gnétales, leurs fleurs et leur position systématique. Ann. Sci. Nat. Bot. IX. **16**:55–185. *figs. 40*. 1912.

witschia and *Amentales* belong to the same lateral phylum, the former at its base, the latter at its summit; that by comparing *Welwitschia* on the one hand with gymnosperms and on the other with angiosperms one may obtain a rough reconstruction of the characters of proangiosperms.

The crux of this whole argument is the interpretation given to the inner, micropyle-forming integument as of carpellary nature. If this is true, no other testimony is needed; and if it is not true, then no other testimony can show the angiosperm level. As stated in the former notice, this contention in the main brings us back to the old conflict over gymnospermy. It is clear that *Welwitschia* is a member of a reduction series, and one can imagine an open ovary derived from a closed one, for there are open ovaries among angiosperms; but it is not easy to imagine a reversion to such structures as archegonia, etc., unless proangiosperms may have retained archegonia in stages of elimination.

It will be interesting to note the disposition made of *Gnetum* and especially of *Ephedra* in the subsequent papers.—J. M. C.

Investigations on Coprinus.—WEIR[15] reports a series of miscellaneous investigations on various species of *Coprinus*. He finds that the deliquescence of these forms is brought about by the action of digestive enzymes and goes on entirely without the aid of bacteria. The digestive enzymes are most abundant when the fruit bodies approach maturity. The various parts of the fungus show considerable differences in resistance to the action of these enzymes. None of the young tissues are affected by extracts of older individuals. Parts of the gills and pileus of older plants, however, are readily dissolved, while the stems are not much affected. Other enzymes whose presence was shown by appropriate methods are tyrosinase, peroxidase, catalase, emulsin, amidase, diastase, coagulase, invertase, cytase, pectase, lipase, and rennetase.

The rest of the paper deals mostly with questions of experimental morphology, and more particularly with the relation between the capacity for regeneration of these fungi first pointed out by BREFELD, and the degree of differentiation of the regenerating tissues. It is found that in the very young fruit body the power of regeneration is not localized, but that all parts are capable of producing new plants from all cut surfaces. In the young cut stem, pilei grow out most readily from the pith, but later, when the pith has disappeared, the regenerating zone moves outward toward the periphery. In the pileus, regeneration takes place most readily at first in the region which is to become the hymenium, and later in the trama. The cuticle is not capable of regeneration. Plants whose pilei were imbedded in plaster or stems whose upper parts were thus imbedded, after removal of the pilei, produced new outgrowths along the lower part of the stems. Attempts at grafting parts of fungi on other individuals of the same species succeeded easily and gave

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[15] WEIR, JAMES R., Untersuchungen über die Gattung *Coprinus*. Flora **103**: 263–320. *figs. 25*. 1911.

interesting results. All parts of *Coprinus* and other fungi exhibit distinct polarity, so that when parts of stems or pilei are grafted in their normal position on the corresponding parts of other individuals used as stocks, union readily takes place by anastamosing of the hyphae. When the part used as the scion is inserted in the reverse position, no union takes place. In partly resupinate forms, like *Polystictus*, polarity was exhibited in the same sense, but portions near the margins showed polarity to a less degree than the older parts.—H. HASSELBRING.

Lagenostoma.—This paleozoic type of seed, the first to be connected with Cycadofilicales, has been investigated further by Miss PRANKERD[16] from preparations of *L. ovoides*. The *Lagenostoma* type of seed has peculiarities that are hard to relate to the structures of the more modern gymnosperm seeds, and any additional knowledge of the facts is welcome. The structures revealed by these new preparations are described in detail, and some interesting "theoretical suggestions" are made. The seed investigated strengthens the suggestion of OLIVER and SCOTT that the outer fleshy layer of the cycadean testa represents the cupule of *Lagenostoma*, the stony layer being developed after fusion of the *Lagenostoma* integument with the cupule. The method of pollination is discussed also, and the curious supposition that extraneous water must be brought to the pollen chamber for the swimming sperms is continued. The facts in reference to the peculiar "crevice-like" pollen chamber are somewhat cleared up. It is shown that the contact of the "central cone" with the outer layer of the nucellus is quite variable, so that apparent continuity might be developed in a variety of ways. The point of this is that a preparation showing a space below and continuity aboves does not prove necessarily that the pollen chamber is being formed from below upward. In certain specimens this very appearance was observed and yet there were pollen grains in the chamber. It is not even certain that the crevice-like chamber was continuous around the central cone. The specialized apical portion of the nucellus is called the "lagenostome," and the suggestion as to its morphology is very interesting. Miss PRANKERD sees in it a modified apical annulus, which in the fossil *Seftenbergia* is a multiseriate structure, but which in living forms has become simpler. If this be true, we have a fern connection for the structure that seemed to be hopelessly advanced, namely the seed.—J. M. C.

The foliar ray of dicotyledons.—BAILEY[17] has followed up his previous work on the rays of certain groups by a more comprehensive study of the dicotyledons, resulting in some important conclusions. The primitive angio-

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[16] PRANKERD, THEODORA L., On the structure of the paleozoic seed *Lagenostoma ovoides* Will. Jour. Linn. Soc. London **40**:461–490. *pls. 22–24. figs. 3.* 1912.

[17] BAILEY, IRVING W., The evolutionary history of the foliar ray in the wood of the dicotyledons, and its phylogenetic significance. Ann. Botany **26**:647–661. *pls. 62, 63.* 1912.

sperms, possessing a siphonostele with strong development of secondary wood, had uniseriate or linear rays, such as characterize the conifers. During the warmer climate of the Mesozoic, "sheets of storage tissue were built up from congeries of uniseriate rays about the persistent leaf traces of evergreen angiosperms. This primitive type of foliar ray has persisted in certain species of primitive families (Casuarinaceae, Fagales, etc.). Later changes in climate modified the storage conditions, and in the majority of living dicotyledons the aggregated units of foliar ray tissue have been diffused through the stem, and in general the evidence of their former relation to leaf traces has disappeared. In a small number of forms the primitive aggregate type has been "progressively compounded or solidified," and the result is the compound or multiseriate ray (deciduous oaks, etc.). In many families there has been a reversion to the primitive uniseriate condition. As a consequence, in the modern species the foliar ray of the primitive aggregate type has been or is being reduced, diffused, or compounded. The evidences of reduction are interesting and important in any scheme of classification. For example, *Castanea* and *Castanopsis* are reduced members of the oak family, and *Alnus mollis* and *A. acuminata* are reduced species of *Alnus*.

It is increasingly evident that the woody cylinder of angiosperms is very far from being a structure of phylogenetic simplicity.—J. M. C.

Bog vegetation.—In studying the various problems connected with the peat bogs of Ohio, DACHNOWSKI[18] has made a careful enumeration of the various plant associations involved, and traced the variously modified successions which occur. Fortunately he has not been content with observations, but has attempted various lines of quantitative study of the factors involved, such as the height and variation of the water table, the acidity of the soil, and the evaporating power of the air. He has also begun a series of chemical analyses of bog water and peat soils. The preliminary results[19] are valuable as being suggestive of lines for future investigation rather than as affording solutions for any existing problems. The chemical changes which take place in the transformation of vegetable matter into peat are only imperfectly understood, but as they are observed as exhibited in passing from the imperfectly formed fibrous material to the competely transformed structureless peat there is a relative loss of oxygen and hydrogen and an increase of carbon and nitrogen simultaneously with an increase in the reducing processes in the soils. The complexity of the problem of relating the vegetation to the chemical nature of the substratum is indicated, as well as the possible importance of the decomposition products of proteids and carbohydrates that are now beginning to be isolated and identified.—GEO. D. FULLER.

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[18] DACHNOWSKI, A., The succession of vegetation in Ohio lakes and peat deposits. Plant World **15**:25–39. 1912.

[19] ———, The relation of Ohio bog vegetation to the chemical nature of peat soils. Bull. Torr. Bot. Club **39**:53–62. 1912.

Germination of teleutospores.—In order to throw some light on the parallelism between the time period during which teleutospores are capable of germination and that during which their host plants can be infected, DIETEL[20] has, in a general way, studied some of the factors influencing the germination of teleutospores of *Melampsora*. Early in March the teleutospores of *Melampsora Larici-Caprearum* Kleb. germinate in about three days when brought into a higher temperature. The time required for germination decreases as the season progresses. Whether the shortening of the period required for germination was due to temperature changes or to a kind of after-ripening of the spores independent of the temperature was not determined. Temporary drying hastened germination. Temporary freezing did not retard the process. Strong light delayed germination. Germination takes place at temperatures as low as 6° C., and only in the neighborhood of this low point was any influence of temperature observed. Experiments with *M. Tremulae* seemed to indicate that germination in this form is less influenced by drying than in *M. Larici-Caprearum*. Germination takes place at temperatures of 6°–10° C., but proceeds more rapidly at 15°–20° C.—H. HASSELBRING.

Seedling structure in Leguminosae.—COMPTON[21] has made a notable contribution to our knowledge of seedling structure. He has examined 201 species of Leguminosae, ranging through all the regions of that vast family. The three parts of the paper present the detailed descriptions, the summarized information, and the general discussion. Under the last head the following topics are considered: the nature of the hypocotyl, hypogeal and epigeal germination, the epicotyl in the Vicieae, the level of the transition, the level of transition and the mature habit, the level of transition and phylogeny, the type of symmetry, plumular traces in hypocotyl and root, tetrarchy, reduction of the number of protoxylems, triarchy, other types of symmetry, the relationships of the types of symmetry, the size of the seedling, the primitive habit. It is obvious that in so extensive a work no outline of the results can be given, and we commend those interested to the 14 conclusions stated by the author. The closing sentence is significant: "To a limited extent, therefore, characters of seedling structure may be of diagnostic value; but it is exceedingly risky to apply them to solve the broader problems of phylogeny."—J. M. C.

Effect of tarred roads on vegetation.—With the extension of the use of gas-tar, petroleum, and bituminous substances for surfacing roads, especially in public parks, the question of injury to plants by these substances becomes one of importance. While many experiments have shown that plants are easily damaged by the fumes of tar and similar substances, such experiments

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[20] DIETEL, P., Versuche über die Keimungsbedingungen der Teleutosporen einiger Uredineen. Centralbl. Bakt. II. **31**:95–106. 1911.

[21] COMPTON, R. H., An investigation of the seedling structure in the Leguminosae. Linn. Soc. Jour. Bot. **41**:1–122. *pls. 1–9*. 1912.

have as a rule been conducted from a laboratory standpoint, and have left unanswered the question of the slow action of these substances under natural conditions. From a study of the effects resulting to vegetation along the tarred roads in some of the parks of Paris, GATIN[22] finds that considerable damage is done to trees and other plants by the tar-laden dust particles; accordingly the injury is less severe along the less frequented roads. A peculiarity of the injury is that it develops very gradually, and in case of the trees did not appear until the practice of surfacing the roads with tar had been continued for two years. Dust collected from tarred roads and dusted at frequent intervals on nursery stock produced characteristic injury, consisting of spotting and browning of the leaves and retardation of growth.—H. HASSELBRING.

Cystidia as hydathodes.—As a result of a critical examination of the cystidia occurring in the hymenium and similar cystidia-like trichomes often found distributed over other surfaces of the fruit bodies of Hymenomycetes, KNOLL[23] concludes that, with the exception of certain special types like the large cystidia of some species of *Coprinus*, these two sets of trichomes belong in a physiological-anatomical sense to the same category of organs, and that they function exclusively as hydathodes. KNOLL finds that the exudation of water is restricted to a definite region, with few exceptions, situated at the apex of the trichome. The cell wall at this point is capable of swelling to such an extent that it forms a colloidal solution in the excreted water. That the drops adhering to the ends of the hydathodes consist of a colloidal solution is shown by the gelatinous residue left when the drops are allowed to evaporate on a glass slide, and also by the fact that a membrane is precipitated when the cystidium with the attached drop is immersed in alcohol. Crystals are often deposited on the ends of the hydathodes as a result of evaporation of the liquid. —H. HASSELBRING.

Plant diseases of Texas.—A survey of the plant diseases occurring within a radius of 100 miles of San Antonio, Texas, has been published by HEALD and WOLF.[24] The paper is based on collections made by the writers during a period of about two years, from 1908 to 1910. It comprises a list of fungi collected on about 200 species of hosts within the region examined, together with brief descriptions of the fungi and notes on the effects produced on the hosts. A number of well executed plates accompany the text; however, the motive that

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[22] GATIN, C. L., Die gegen die Abnutzung und den Staub der Strassen angewendeten Verfahren und ihre Wirkung auf die Vegetation. Zeitschr. Pflanzenkrank. **22**:193–204. 1912.

[23] KNOLL, F., Untersuchungen über den Bau und die Funktion der Cystidien und verwandter Organe. Jahrb. Wiss. Bot. **50**:453–501. *figs. 69*. 1912.

[24] HEALD, F. D., and WOLF, F. A., A plant disease survey in the vicinity of San Antonio, Texas. Bur. Plant Ind. Bull. 226. pp. 112. *figs. 2*. *pls. 19*. 1912.

guided the writers in their selection of material for illustration is not clear. As a list of parasitic fungi from a region where little systematic collection has been carried on, this paper is a useful contribution. Its usefulness might have been greatly enhanced if the authors had indicated what part of their material constituted additions to the known fungus flora of Texas, and what part represented species formerly known from that region, for it can scarcely be doubted that so extensive a collection of material contains much that is new to the region.—H. HASSELBRING.

A new type of Cycadofilicales.—From a study of numerous casts, SCHUSTER[25] has described the staminate and ovulate flowers of *Schuetzia anomala* and has drawn some conclusions in regard to the position of the genus. The impressions of the staminate flowers were so numerous that it was not difficult to make reconstructions. The flower consists of 12–20 cyclic sporophylls united throughout the lower two-thirds of their length and bearing sporangia upon their inner surfaces, resembling SÉLLARD'S *Codonotheca* and STUR'S *Calymmatotheca*. The flowers are in a spicate inflorescence. The longitudinally striated "seeds" described by GOEPPERT are regarded as megasporophylls, and it is important to note that these megasporophylls are in undoubted connection with twigs bearing conifer-like leaves. On account of this association, SCHUSTER would make *Schuetzia* the type of a new group of Cycadofilicales, characterized by the conifer-like leaves.—CHARLES J. CHAMBERLAIN.

Root nodules of Podocarpineae.—Miss SPRATT[26] has found that root nodules are present in *Podocarpus*, *Microcachrys*, *Dacrydium*, *Saxegothaea*, and *Phyllocladus*, being modified lateral roots. A root-hair is penetrated by *Pseudomonas radicicola* (a nitrogen-fixing organism) and from thence enters the cortex. In all cases the nodules are produced by the infection of the meristematic tissue of the young lateral root before it emerges from the cortex of the parent root. Many interesting observations are made upon the stages of the bacteria and also upon the condition of the tissues of the host. The conclusion is suggested that the morphology of the nodules favors the view that *Podocarpus* and *Saxegothaea* "are the most widely divergent of the genera in the Podocarpineae, and that they are connected through *Microcachrys* and *Dacrydium*." The presence of the nodules in *Phyllocladus* is also further confirmation that the genus is related to the podocarps rather than to the taxads. —J. M. C.

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[25] SCHUSTER, J., Über die Fruktification von *Schuetzia anomala*. Sitzungsb. Kaiserl. Akad. Wiss. Wien **120**:1125–1134. *pls. 1, 2.* 1911.

[26] SPRATT, ETHEL ROSE, The formation and physiological significance of root nodules in the Podocarpineae. Ann. Botany **26**:801–814. *pls. 77–80.* 1912.

Morphology of Uvularia.—Miss ALDEN[27] has investigated the life history of *Uvularia sessilifolia*, chiefly as to the sequence of events, presumably in the region of New York City. The archesporium of the microsporangium (3–6 cells) becomes differentiated the first of August, at which time also the division into parietal and sporogenous series occurs. Mature microspore mother cells were found in the middle of September, and the tetrad divisions occurred in October, so that the winter is passed with the microspores fully formed. In the latter part of the following April the division of the microspore nucleus into generative and tube nuclei occurs, and probably the former divides after the shedding of pollen. The archesporium of the megasporangium is differentiated early in March (seven months later than the microsporangiate archesporium), and consists of a single hypodermal cell which does not cut off a parietal cell. The reduction division occurs the last week of April.—J. M. C.

Spermogonium and fertilization in Collema.—Miss BACHMANN[28] has investigated *Collema pulposum* as to the nature of the spermatia and its bearing on the question of functional sexuality among the Ascomycetes. The spermatia of this species are not born in spermogonia, but few in number upon a hypha below the surface of the thallus, being completely imbedded and never set free. The carpogonia resemble those of other lichens in general structure, but the long end cell of the trichogyne does not grow toward the surface of the thallus, but more or less horizontally within the thallus toward the region of the spermatia. The attraction of the spermatia for the trichogynes is shown by the convergence of the latter about a group of spermatia. The spermatium fuses with the trichogyne to which it has become attached, and the subsequent changes are those that have been described. It seems evident that in this case the spermatia and trichogyne are functional.—J. M. C.

Seedling anatomy of Sympetalae.—LEE[29] has investigated the seedling anatomy of Convolvulaceae, Polemoniaceae, Hydrophyllaceae, Boraginaceae, Labiatae, Solanaceae, Scrophulariaceae, Bignoniaceae, and Acanthaceae. The extent of the transition region is related in a general way to the size of the seedlings, which varies greatly in different species. In the smaller seedlings the transition region is short, and the rearrangements are concluded in the upper part of the hypocotyl; while in the larger seedlings the transition region is very extended. Cotyledonary tubes occur in members of all the families,

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[27] ALDEN, ISABEL, A contribution to the life history of *Uvularia sessilifolia*. Bull. Torr. Bot. Club **39**:439–446. *pls. 34, 35.* 1912.

[28] BACHMANN, FREDA M., A new type of spermogonium and fertilization in *Collema*. Ann. Botany **26**:747–760. *pl. 69.* 1912.

[29] LEE, E., Observations on the seedling anatomy of certain Sympetalae. I. Tubiflorae. Ann. Botany **26**:727–746. *pl. 68.* 1912.

but their presence seems to have nothing to do with the transition phenomena. The prevailing type of transition, present in all the smaller seedlings, is VAN TIEGHEM's type 3. Internal phloem was present in all the Solanaceae and Convolvulaceae examined, with a few possible exceptions.—J. M. C.

A disease of sugar cane.—The sugar plantations of Hawaii have suffered greater loss from an endemic disease called "iliau" than from all other fungous diseases combined. LYON, now at the Experiment Station of the Hawaiian Sugar Planters' Association, has investigated the disease[30] and finds that the causal organism is a new species of *Gnomonia* (*G. iliau*), the imperfect stage being *Melanconium*. The *Gnomonia* form is infrequent, while the *Melanconium* form is of constant occurrence. It is a leaf-sheath disease, and its attack makes it a disease of young shoots only. The entrance is effected through the leaf-bases inserted on the stem below the soil surface, and thence it extends upward and inward. The tightly packed roll of leaf-sheaths surrounding the young stem-tip is cemented into a rigid cone, so that it is impossible for the stem-tip to escape.—J. M. C.

Diaphragms in air passages.—LE BLANC[31] has reviewed the literature on the diaphragms occurring in various aquatic plants and examined other species in order to discover the origin, manner of development, and function of these organs. One of the most peculiar features of these plates is the occurrence of perforations in the form of peculiar intercellular spaces caused by the diminution of the cell contents and the consequent contraction of the cells. These perforations permit free gas exchange and yet do not greatly detract from the rigidity of the diaphragms. The diaphragms do not seem to be due to any reaction toward the aquatic medium in which the plants develop, and appear to be a portion of the mechanical tissue system occasionally containing some reserve food materials.—GEO. D. FULLER.

Algae of Colorado.—ROBBINS[32] has published a list of the algae of Colorado, which brings together all the recorded species and the additions made by the author during three years of investigation. The result is a list of 143 species, including 38 Cyanophyceae and 105 Chlorophyceae. *Spirogyra*, with 14 species, is the largest genus.

The same author[33] has investigated also the occurrence of algae in certain

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[30] LYON, H. L., Iliau, an endemic cane disease. Exper. Sta. (Hawaii) Bull. 11. pp. 32. *figs. 10. pl. 1* (colored). 1912.

[31] LE BLANC, M., Sur les diaphragmes des canaux aérifères des plantes. Rev. Gén. Bot. **24**: 233–243. 1912.

[32] ROBBINS, W. W., Preliminary list of the algae of Colorado. Univ. Colorado Studies **9**: 105–118. 1912.

[33] ———, Algae in some Colorado soils. Col. Agric. Exper. Sta. Bull. 184. pp. 24–36. *pls. 4.* 1912.

soils in which *Azotobacter chroococcum* is extremely active in fixing nitrogen. By the use of cultures, which are described, 21 species of soil algae were found, all but two being Cyanophyceae, and the best represented family being Nostocaceae. It is concluded that these algae are an important source of energy for *Azotobacter*.—J. M. C.

Podozamites distans.—The fragments referred to this form, sometimes under the name of *Cycadocarpidium*, have been regarded by some as pinnate leaves, and by others as shoots with spirally arranged leaves. The megasporophylls, with two ovules at the base, bearing some resemblance to those of *Dioon*, are collected into a loose cone. Nevertheless, SCHUSTER[34] comes to the conclusion that *Podozamites distans* is a primitive conifer, coming from the same Cycadofilicales stock which gave rise to the Ginkgoales. Consequently, he would have *Podozamites* removed from the Cycadales and placed with Coniferales. SCHUSTER's figures, as well as two of NATHORST's which he reproduces, seem to the reviewer to favor relationship to the Cycadales.—CHARLES J. CHAMBERLAIN.

Anatomy of Equisetum.—Lady ISABEL BROWNE[35] has investigated the anatomy of the strobilus and of the fertile stem of *Equisetum*. The xylem situation in this genus is of great interest, and in the axis of the strobilus it is best developed. At the nodes, the xylem forms a ring or occurs as bands of varying width; while in the internodes the xylem breaks up into definite strands. *E. arvense*, *E. palustre*, and *E. limosum* form a series showing progressive reduction of the xylem. The study of the strobilus further confirms the view that the "sporangiophores" are not lobes of a suppressed foliar member, but are "whole appendages," which would seem to indicate that they are not sporangiophores.—J. M. C.

Stomata of Bennettites.—LIGNIER[36] has discovered the existence of stomata on the interseminal scales of *Bennettites Morieri*. The structure as figured is obvious enough, and about the guard cells there are concentric subsidiary cells. LIGNIER raises the question whether the presence of these stomata does not indicate freedom for the movement of air among scales and ovules, and therefore less compactness of structure than develops later, when the seeds mature and the tips of the interseminal scales hypertrophy. Since stomata occur within the ovaries of angiosperms, as *Lilium* for example, their presence does not prove the free circulation of air.—J. M. C.

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[34] SCHUSTER, JULIUS, Bermerkungen über *Podozamites*. Ber. Deutsch. Bot. Gesells. **29**:450–456. *pl. 17*. 1911.

[35] BROWNE, ISABEL M. P., Contributions to our knowledge of the anatomy of the cone and fertile stem of *Equisetum*. Ann. Botany **26**:663–703. *pls. 64, 65. figs. 10*. 1912.

[36] LIGNIER, O., Stomates des écailles interséminales chez le *Bennettites Morieri* (Sap. et. Mar.). Bull. Soc. Bot. France **59**:425–428. *figs. 2*. 1912.

Classification of plants.—A third edition of Professor BESSEY's *Outlines of plant phyla* has appeared. The previous editions were noted in this journal (**51**:317. 1911; **53**:275. 1912) and the general features of the classification given. In the new edition the 14 phyla remain the same, but the families have increased from 648 to 652. The relation of the conventional four great groups to this scheme may be indicated by the statement that the thallophytes are broken up into 7 phyla, the bryophytes remain as a single phylum, the pteridophytes become 3 phyla, and the spermatophytes 3.—J. M. C.

Perithecium of Polystigma.—BLACKMAN and WELSFORD[37] have investigated the development of the perithecium of *Polystigma*, and have discovered that while well marked ascogonia occur, they disorganize without producing ascogenous hyphae, and that the spermatia are also functionless. It differs from most of the Ascomycetes in which the normal sexual process is absent by the fact that both sex organs are distinctly produced, but that both are abortive.—J. M. C.

Wound reactions in fern petioles.—HOLDEN[38] induced wound reactions in the petioles of 37 species of ferns, the wounds being thin superficial shavings made with a scalpel in three regions: the curled apical portion, the region of pinna insertion, and the region below pinna insertion. Various reactions were obtained, which differ too much in details to be summarized in a review, but all of which are interesting contributions to the subject of wound reactions.—J. M. C.

Mycorhiza of Asarum.—SCHWARTZ[39] has studied the mycorhiza of *Asarum europaeum*, finding it limited to the cortical region abutting on the steles of young roots. Thick-walled swellings were found on some of the hyphae, representing a resting stage.—J. M. C.

Lateral archegonia in Pinus.—SAXTON[40] has made the very interesting discovery of a female gametophyte of *Pinus maritima* which bears two lateral groups of two archegonia each, and no terminal (micropylar) archegonia at all.—J. M. C.

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[37] BLACKMAN, V. H., and WELSFORD, E. J., The development of the perithecium of *Polystigma rubrum* D.C. Ann. Botany **26**:761–767. *pls. 70, 71.* 1912.

[38] HOLDEN, H. S., Some wound reactions in filicinean petioles. Ann. Botany **26**:777–793. *pls. 73, 74. fig. 1.* 1912.

[39] SCHWARTZ, E. J., Observations on *Asarum europaeum* and its mycorhiza. Ann. Botany **26**:769–776. *pl. 72.* 1912.

[40] SAXTON, W. T., Note on an abnormal prothallus of *Pinus maritima* L. Ann. Botany **26**:943–945. *fig. 1.* 1912.

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Classified entries will be found under Contributors and Reviews. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italic*.

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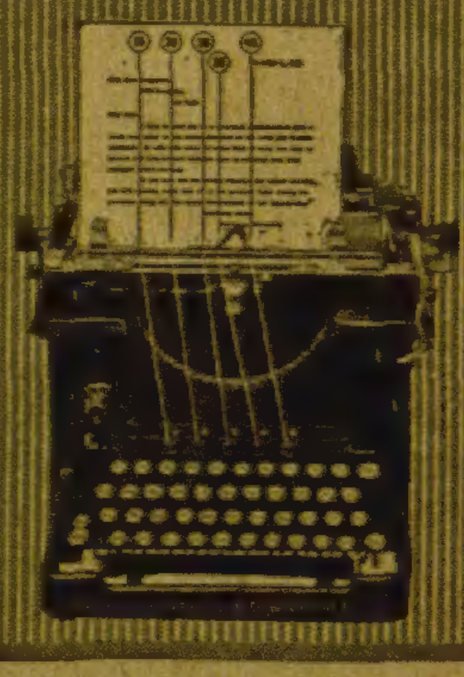

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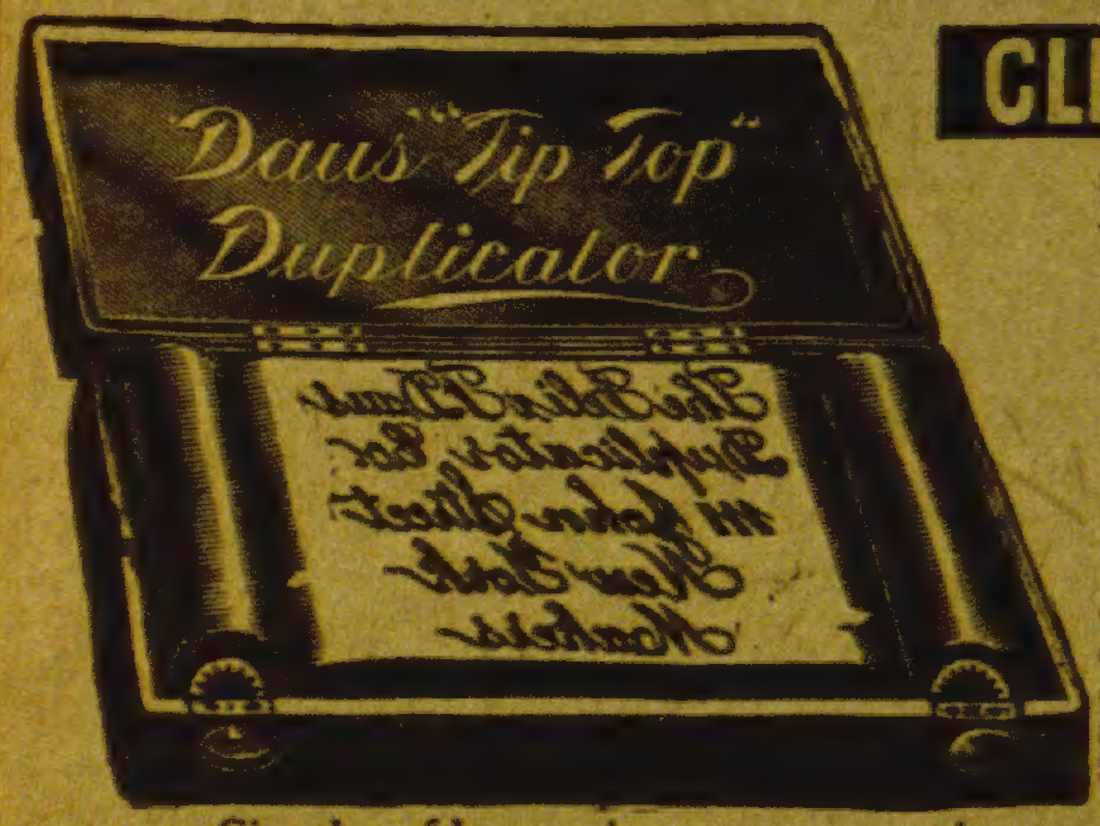

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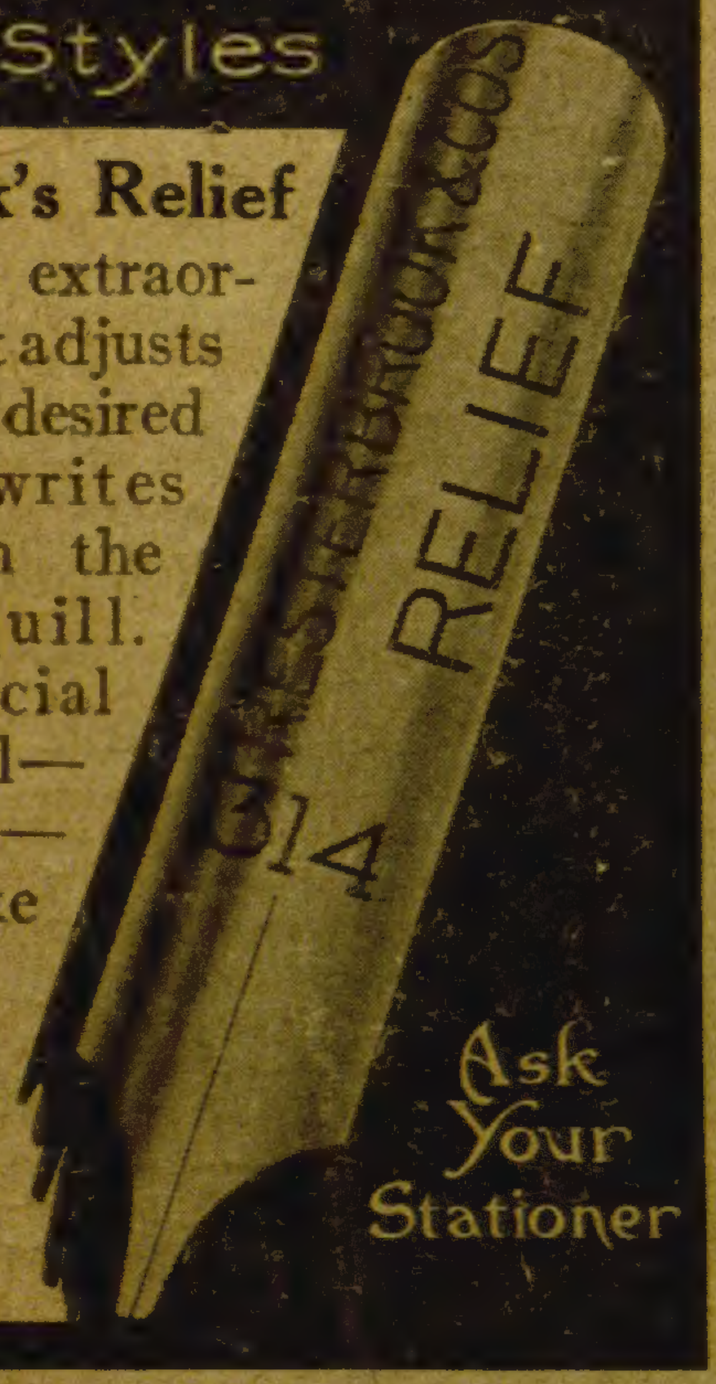

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